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Building on Beverton's legacy: life history variation and fisheries management

Québec, Quebec, Canada
11–14 August 2003

[Construire sur l'héritage de Beverton : variation du cycle biologique et gestion des pêches]

Québec (Québec) Canada
11–14 août 2003

Guest Editor

Brian J. Shuter
Ontario Ministry of Natural Resources
and Department of Zoology
University of Toronto
Toronto, Ontario

Peter A. Abrams
Department of Zoology
University of Toronto
Toronto, Ontario

Directeur scientifique invités

Brian J. Shuter
Ministère des Richesses naturelles de l'Ontario
et Département de zoologie
Université de Toronto
Toronto (Ontario)

Peter A. Abrams
Département de zoologie
Université de Toronto
Toronto (Ontario)

INTRODUCTION / INTRODUCTION

Introducing the symposium "Building on Beverton's legacy: life history variation and fisheries management"[1]

Brian J. Shuter and Peter. A. Abrams

Abstract: Throughout his career, Ray Beverton displayed an interest in the life history diversity in marine and freshwater fish. The papers collected here describe recent research directed at documenting this diversity and understanding both its consequences and the processes that generate it. There are three themes: factors that direct life history dynamics; fishing as a force that redirects life history dynamics; and roles for life history statics in conservation management. The "dynamics" papers show that fish life histories can evolve in response to both natural and harvest-induced selective pressures. Evolution in response to harvesting can be rapid, with potentially dramatic effects on population dynamics and sustainable exploitation. The "statics" articles demonstrate how maturity traits combine with shifts in habitat use to shape the sensitivity of a population to habitat loss. Life history shifts can dramatically alter the safety of harvesting policies that were prudent in the past; shifts of the predators or prey of a harvested species can be as important as shifts in the harvested species itself. Further work on the ecological circumstances that favour different degrees of plastic or genetic life history responses to human impacts are needed to prevent inadvertent induction of long-lasing evolutionary changes in fish life histories.

Résumé : Au cours de toute sa carrière, Ray Beverton s'est intéressé à la diversité des cycles biologiques chez les poissons de mer et d'eau douce. Les articles rassemblés dans ce numéro portent sur des recherches récentes qui visent à illustrer cette diversité et à en comprendre tant les conséquences que les processus générateurs. Il y a trois thèmes, les facteurs qui régissent la dynamique des cycles biologiques, le rôle de la pêche dans la réorientation de cette dynamique et l'importance des paramètres statiques du cycle biologique dans la gestion de la conservation. Les articles sur la dynamique montrent que les cycles biologiques des poissons peuvent évoluer en réaction aux pressions sélectives générées aussi bien par le milieu naturel que par la récolte. L'évolution en réaction à la récolte peut être rapide et avoir des effets potentiellement spectaculaires sur la dynamique des populations et l'exploitation soutenable. Les articles sur les paramètres statiques démontrent comment certaines caractéristiques de la maturité se combinent à des changements dans l'utilisation de l'habitat pour déterminer la sensibilité d'une population à la perte d'habitat. Les modifications dans les cycles biologiques peuvent altérer de façon importante la sécurité de politiques de pêche qui s'étaient avérées prudentes dans le passé; les modifications chez les populations de prédateurs ou de proies d'une espèce récoltée peuvent avoir autant d'importance que les modifications chez l'espèce récoltée elle-même. Pour éviter d'introduire involontairement des changements évolutifs de longue durée dans les cycles biologiques, il est nécessaire de mener plus de recherches sur les conditions écologiques qui favorisent les diverses intensités de réactions plastiques ou génétiques dans les cycles en réactions aux impacts anthropiques.

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B.J. Shuter.[2,3] Harkness Laboratory of Fisheries Research, c/o Aquatic Research and Development Section, Ontario Ministry of Natural Resources, 300 Water Street, Peterborough, ON K9J 8M5, Canada.
P.A. Abrams. Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada.

[1]This article was part of a special symposium entitled Building on Beverton's legacy: life history variation and fisheries management, which took place on 11–14 August 2003 in Québec, Quebec, during the 133rd annual meeting of the American Fisheries Society.
[2]Corresponding author (e-mail: shuter@zoo.utoronto.ca).
[3]Present address: Aquatic Ecology Group, Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada.

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Introduction

Ray Beverton's long and influential career in fisheries science was marked by a continuing interest in the wide diversity of life history traits evident in both marine and freshwater fish. His publications on this subject span over 45 years (Beverton 1963, 1987, 1992, 1998; Beverton and Holt 1959; Beverton et al. 2004). His paper with Sidney Holt in 1959 provided perhaps the first clear demonstration that strong interspecific correlations link life time growth pattern, reproductive scheduling, and mortality among marine fish species (Beverton and Holt 1959). His most recent posthumous paper (Beverton et al. 2004) documented how fisheries can reshape the average life history of a population through nonrandom selection of individuals that differ in their life histories. Many of Beverton's publications focus on what he called life history statics: the careful quantification of interrelations among fish life history traits and the use of these relations as predictive tools to permit fisheries managers to characterize the dynamics of as yet unstudied populations. The term life history statics implies that the life history of a population is immutable in ecological time; once it is fully characterized (directly through observation or indirectly using one of the predictive tools mentioned above), that characterization can be used in any management planning model for the population. However, Beverton recognized the importance of what he called "life history dynamics", and in one of his last papers he promised to focus more on this important area in the future. Throughout his work in this field, Beverton exhibited a strong interest in the mechanisms that generate and sustain the life history diversity that he was trying to quantify and apply. In his 1963 paper, he offered the following verbal hypothesis regarding these mechanisms:

> "An adaptive interpretation of the adjustment of growth and longevity might be explicable in simple Darwinian terms by supposing that it is an "advantage" to the individual to complete as much as possible of its potential growth within its likely maximum life span, this advantage being that which best enables its reproductive potential to be realized and so maximizes the contribution of its progeny to future generations."

This hypothesis foreshadows much of the recent work in the field, and it underlies many of the papers included in this symposium. These papers deal with both the dynamics and statics of fish life histories. They reflect a new recognition of the importance of studying and understanding life history malleability on relatively short time scales. They provide significant, new empirical support for the possibility raised by Miller (1957) and Ricker (1981) that exploitation itself could drive evolutionary change in the life history of fish stocks, and they provide further affirmation that life history variation in the wild, both within and between fish species, is constrained. These constraints generate repeatable associations between traits that can be quantitatively characterized and are of practical value in fisheries management. We believe the articles in this symposium represent an interesting and useful sample of the broad body of valuable work that has grown out of Beverton's earlier contributions.

Overview of the series

The papers in the symposium present a variety of perspectives on life history variation — its statics and dynamics — in a range of freshwater and marine fish species. Together, they constitute a strong argument for Beverton's view that an evolutionary life history perspective is an essential element of effective resource management. This view rests first on the fact that the life history traits of a species reflect both its evolutionary past and its present population dynamics. Adaptive change in these characteristics renders untenable, important assumptions of classical fisheries management, such as (*i*) population-specific demographic traits are determined independently of each other; (*ii*) population-specific demographics are fixed and immutable; (*iii*) an increase in the abundance of an exploited population is a mark of population recovery and (or) underexploitation; (*iv*) population abundance is relatively insensitive to changes in exploitation rate at, or near, the exploitation level producing maximum sustainable yield.

Perhaps the most important contribution of this set of papers is the extensive, new empirical evidence that exploitation can cause rapid evolution in the average life history traits of a population. These evolved changes are essentially irreversible and often will cause a reduction in sustainable yields and, in the worst case, population extinction.

The papers in the symposium can be grouped under three broad themes: (*i*) the environmental and biological factors that direct life history dynamics (Conover et al. 2005; Shuter et al. 2005; Magnan et al. 2005; Abrams and Matsuda 2005; Rennie et al. 2005; DeAngelis et al. 2005); (*ii*) fishing as a selective force that can redirect life history dynamics (Reznick and Ghalambor 2005; Munch et al. 2005; Olsen et al. 2005; Hutchings 2005; Rijnsdorp et al. 2005; Dunlop et al. 2005); and (*iii*) new roles for life history statics in conservation management (Reynolds et al. 2005; Gerber et al. 2005; Winemiller 2005; Rose 2005). The "dynamics" articles present both theoretical arguments and empirical evidence demonstrating that the life history traits of species can change slowly in response to a variety of selective pressures, but that exploitation is capable of eliciting rapid change, with potentially dramatic effects on population dynamics and sustainable harvests. The "statics" articles demonstrate how traditional life history traits (age and (or) size at maturity), combined with known age- or size-dependent shifts in habitat use, to shape the sensitivity of a population to environmental degradation.

Theme 1: the environmental and biological factors that direct life history dynamics

Conover et al. (2005) provide a broad overview of the environmental and ecological forces that have shaped the natural patterns of life history variation evident in Atlantic silverside (*Menidia menidia*) populations over their extensive geographic range along the east coast of North America. They argue that this variation reflects local genetic adaptation to differences in food availability and predation pressure. They show experimentally that intense size-selective predation, which targets fast-growing genotypes (and mimics common patterns of fishing mortality), is capable of rapidly

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producing a heritable decrease in size at maturity. Shuter et al. (2005) use recently developed theory regarding optimal growth trajectories (Lester et al. 2004) to show that the higher mortality rates suffered by mid-trophic-level fish in freshwater lakes can explain the higher reproductive investment and reduced adult growth that these fish exhibit relative to top predators in the same lakes. These results confirm some of Beverton's ideas on how selective forces constrain life history dynamics in ways that create the commonly observed correlations between life history traits. Magnan et al. (2005) examine the impacts of both fishing mortality and interspecific competition on the life histories observed in different populations of brook trout (*Salvelinus fontinalis*). The age at maturity of males and females was found to be inversely related to the intensity of both fishing and interspecific competition. Both of these factors reduced survival, but did not appear to affect growth. Neither factor affected reproductive effort. Abrams and Matsuda (2005) use mathematical models to show how adaptive shifts in the reproductive effort of a prey species can alter its predator's response to increasing harvest. The prediction is that predators can ultimately increase in population size in response to increased fishing pressure, as a result of the increased productivity in the prey population that follows from the prey's life history shift. This outcome can occur whether the life history shift is caused by phenotypic plasticity, evolutionary change, or shifts in the relative abundances of prey species having different life history traits. Rennie et al. (2005) provide an empirical demonstration of the role that predation threat may play in shaping the growth rates of yellow perch (*Perca flavescens*), with consequent implications for other perch life history traits. Such alterations in growth rates could be important in regulating the harvest of predators of perch, as suggested by the models of Abrams and Matsuda. In a study with broad theoretical and practical application, DeAngelis et al. (2005) use empirical and simulation studies of the fish communities that persist among the temporary and permanent habitat patches of the Florida Everglades to show that spatial and temporal variability in the presence–absence of useable habitat will promote and sustain diversity in life histories among species competing for the same resources because that diversity permits those species to coexist.

Theme 2: fishing as a selective force that can redirect life history dynamics

Reznick and Ghalambor (2005) summarize previous field experiments with Trinidadian guppies (*Peocilia reticulata*) that demonstrate rapid evolutionary change in growth rate and (or) age and size of maturity in response to changes in mortality schedules produced by manipulating predator densities. These changes were consistent with the natural patterns of variation in maturity and mortality that were evident in undisturbed populations found near the field sites. Reznick and Ghalambor argue that guppy communities provide a convenient and useful model system for studying the long-term impacts of exploitation. Munch et al. (2005) take a broader look at the responsiveness of different traits to the selective pressures imposed by size- (or growth-) related harvesting and show that traits expressed early in life seem to evolve at a much slower rate than do adult characteristics. Understanding the selective pressures and heritabilities of a variety of life history traits is likely to be required for informed management of species adapting to a changed or changing environment. Olsen et al. (2005) and Hutchings (2005) both discuss the case of cod (*Gadus morhua*) in the North Atlantic, where some discrete populations appear to have evolved earlier maturation at a smaller size in response to heavy exploitation. Olsen et al. (2005) show that the relationship between age at maturation and size at maturation has shifted significantly during the recent period of very heavy fishing pressure. Hutchings (2005) shows that the reduced reproductive rate of adults under the current life history will make recovery from low stock sizes much slower and less certain than it would have been in the absence of the apparent evolutionary shift. Rijnsdorp et al. (2005) show that age and size of maturity and reproductive investment in North Sea plaice (*Pleuronectes platessa*) stocks have also changed in recent decades, again apparently in response to heavy exploitation. It is important to understand the reversibility of such life history shifts and the potential time required for such a reversal. This issue requires that we know the genetic or phenotypic basis of the shift, something that is difficult to discern in the absence of controlled, "common garden" rearing experiments. Olsen et al. (2005) feel that the life history shifts in cod are likely to have a genetic basis; however Dunlop et al. (2005) show that a quite striking divergence in the mean life history traits of smallmouth bass (*Micropterus dolomieu*) introduced into two lakes a century ago is unlikely to represent genetic divergence; despite 100 years of selection, both bass populations still exhibit approximately the same between-individual relationship between age and size of maturity.

Theme 3: new roles for life history statics in conservation management

Reynolds et al. (2005) describe an empirical study of unexploited European freshwater fish that demonstrates that differences in life history traits are of little value in identifying species whose persistence is threatened by wide-scale habitat destruction. This contrasts with the usefulness of these traits as indicators of population sensitivity to overexploitation.

In a simulation study, Gerber et al. (2005) examine the relative effectiveness of no-harvest areas compared with harvest controls in protecting species characterized by four alternative life histories and several alternative patterns of transition between different life stages and different obligate habitats. Their results suggest that species with both high reproductive rates and larval dispersal (e.g., sea urchins (*Tripneustes ventricosus*) and goliath groupers (*Epinephalus itajara*)) show the highest population recovery rates following implementation of no-harvest areas. Winemiller (2005) argues that the broad classification of life history traits proposed by Winemiller and Rose (1992) is sufficient to provide reliable information on the strength of density dependence at the population level and that this kind of information is useful in dealing with issues of conservation and the efficacy of supplemental stocking. Winemiller's 1992 coauthor, Ken Rose, has a somewhat less sanguine view of the predic-

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tive power of their original three-strategy model for issues related to harvesting (Rose 2005). Together these articles give some idea of the potential value of simply documenting life history traits across populations and developing empirical descriptions of the relationships linking these traits. Nevertheless, it is clear that any predictions based on such static relationships will have to be tempered by the recognition that rapid shifts in life history are possible, as documented in the work included in the first sections of this symposium.

Looking to the future

All of the articles in this symposium illustrate the need for further work on the diversity of life history traits in fish communities and, more generally, in biological assemblages. We still need to know much more about the rates and potential magnitudes of life history shifts caused by both behavioural and morphological plasticity. We also need to develop methodologies for distinguishing plastic and evolved changes. The possibility for both types of changes to occur in parallel calls for a more flexible approach to managing exploited and (or) endangered species. Shifts in life history traits may dramatically alter the safety of harvesting policies that might have been prudent in the past. Shifts in the life histories of interacting species — predators or prey of the harvested species — may be as important in this regard as life history shifts are in the harvested species itself. Future study may allow us to determine the ecological circumstances that favour different degrees of plastic or genetic responses of life history traits to both exploitation and other types of environmental change. This should help avoid the risk of adverse evolutionary changes in life histories that may take many generations to reverse.

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PERSPECTIVE / PERSPECTIVE

Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*)[1]

David O. Conover, Stephen A. Arnott, Matthew R. Walsh, and Stephan B. Munch

Abstract: The potential of fishing mortality to cause rapid evolutionary changes in life history has received relatively little attention. By focusing only on ecological responses, standard fisheries theory and practice implicitly assume either that genetic influences on life history in the wild are negligible or that natural selection and adaptation is a slow process that can be effectively ignored. Lack of contrary evidence has allowed these assumptions to persist. Drawing upon >25 years of research on the Atlantic silverside (*Menidia menidia*), we show that adaptive genetic variation in many traits is finely tuned to natural variation in climate. Much of this variation is caused by a gradient in size-selective winter mortality and involves two- to threefold changes in physiological traits that influence population productivity. Many other species are now known to display similar patterns. Harvest experiments show that these traits can evolve rapidly in response to size-selective fishing. Hence, the pool of genotypes that code for life history traits is a highly dynamic property of populations. We argue that the lessons from *Menidia* are applicable to many exploited species where similar observations would be difficult to obtain and advocate greater use of species models to address fundamental questions in fishery science.

Résumé : On s'est peu intéressé à la possibilité que la mortalité due à la pêche puisse entraîner de rapides changements évolutifs dans le cycle biologique. En se concentrant seulement sur les effets écologiques, la théorie et la pratique courantes des pêches présument implicitement ou bien que les influences génétiques sur le cycle biologique en nature sont négligeables ou alors que la sélection naturelle et l'adaptation sont des processus lents qui peuvent en pratique être ignorés. Ces présuppositions ont pu se maintenir en l'absence de preuves contraires. En nous basant sur >25 ans de recherche sur la capucette, *Menidia menidia*, nous démontrons que la variation génétique adaptative de plusieurs caractéristiques est finement ajustée à la variation naturelle du climat. Une partie importante de cette variation est causée par un gradient de mortalité hivernale reliée à la taille et implique des changements de l'ordre de deux ou trois fois dans les caractéristiques physiologiques qui influencent la productivité de la population. Il est maintenant connu que plusieurs autres espèces possèdent des patterns semblables. Des récoltes expérimentales montrent que ces caractéristiques peuvent évoluer rapidement en réaction à la pêche sélective en fonction de la taille. Le pool des génotypes qui sont responsables des caractéristiques du cycle biologique forme donc une propriété très dynamique des populations. Nous croyons que les leçons apprises chez *Menidia* s'appliquent à de nombreuses espèces exploitées chez lesquelles des observations similaires seraient difficiles à faire et nous suggérons une utilisation plus grande en sciences halieutiques des modèles de population qui s'intéressent aux questions fondamentales.

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D.O. Conover,[2] S.A. Arnott, and M.R. Walsh. Marine Sciences Research Center, Stony Brook University, Stony Brook, NY 11794-5000, USA.
S.B. Munch. Department of Applied Mathematics and Center for Stock Assessment Research, University of California, Santa Cruz, CA 95064, USA.

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[2]Corresponding author (e-mail: dconover@notes.cc.sunysb.edu).

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Introduction

Among the first to appreciate the importance of life history variation to fishery science was R.J.H. Beverton. Much of Beverton's work focused on explaining the incredible diversity of life histories in fishes. Some of his most important contributions were that fishery harvest regimes must be tailored to the differences in life history that occur among species or populations (Beverton and Holt 1957), that some life histories are far more susceptible to overfishing than others, and that life history traits are highly intercorrelated across species such that changes in one trait are predictably associated with changes in other traits (Beverton 1992). Beverton's attention was focused primarily on differences among species and populations because at these phylogenetic levels, phenotypic differences are likely to have a genetic component and therefore represent the result of evolutionary divergence rather than environmental influences alone.

The preeminence of the population and (or) species levels as the major sources of genetic variation relevant to fishery management still prevails. We recognize that populations of a species represent unique gene pools or "evolutionary significant units" that have a spatially explicit phylogeographic structure defined by the level of gene flow and within which may exist genetically based adaptations to local environmental conditions. Lineages must therefore be preserved, if threatened with extinction or introduction of alien genotypes, so as to protect the genetic diversity of a species. At the individual level, however, fishery management theory implicitly assumes that phenotypic variation is purely environmental. Essentially, we assume that the effect of harvest on a stock is analogous to mowing a lawn, i.e., removal of biomass stimulates new production for further harvest, without changing the intrinsic characteristics (i.e., the gene pool) of the lawn. But in reality, fishing is a sorting process that selectively removes individuals. Even though the importance of individual genotypic differences has long been recognized in fish breeding and hatchery operations, we have not fully appreciated the fact that genetic variation in nature is organized in a hierarchical fashion beginning first among individuals within populations, then among populations, and then among species. In short, we do not consider individual genotypes to be evolutionary significant units in managing fishery harvests.

Why have we largely ignored genotypic variation in life history in the wild as relevant to harvest management? We offer several reasons. First is the fact that physiological and life history traits are notoriously difficult to observe at the individual level. Unlike morphology or behavior, for example, which can be observed visually, physiological traits in the wild are essentially invisible to us. Instead, we measure physiological traits indirectly through analysis of aggregate measures such as change in mean size or proportion maturing at age. These practices often obscure individual variability. Second is the belief that phenotypic plasticity of physiology and life history at the individual level in nature is so high that genetic influences are easily swamped by environmental influences. Physiological traits like growth rate, for example, vary dramatically with environmental factors such as temperature. We therefore focus attention on extrinsic factors with the greatest apparent impact and, for the sake of simplicity, ignore the rest. For example, bioenergetics models designed to predict fish growth in response to environmental differences are routinely parameterized without regard to genetic differences below the species level, and in fact often borrow parameters across species (Munch and Conover 2002). Such practices assume that genetic effects on physiology at the individual or population level are weak relative to environmental influences and therefore can be safely ignored. Third is the belief that genetic adaptation is a slow process requiring time scales far longer than those of ecological processes. Hence, evolutionary responses to harvest mortality also can be effectively ignored and population dynamics can be modeled as a function of ecological density-dependent responses alone.

What if these premises are wrong? What if within populations there is substantial variation among genotypes that code for life history differences expressed by phenotypes that differ in their susceptibility to fishing, much like species do? What if local adaptation is a rapid process that can occur despite gene flow and on time scales relevant to contemporary management decisions? If so, then we would expect to see in the absence of fishing that adaptive traits are finely tuned to selective agents in nature, that the geography of adaptation is spatially coherent with strong environmental gradients, and that such traits are capable of responding rapidly to selection. In harvested stocks, we would expect to see shifts in life history parameters that reflect the change in fitness caused by the addition of fishing mortality to natural mortality.

In this essay, we address these questions by reviewing what has been learned about life history evolution from >25 years of research on a single model species: the Atlantic silverside (*Menidia menidia*). We first describe the ecology and life history of *M. menidia* in nature, focusing particularly on variation in growth across a latitudinal gradient, its physiological basis, and its adaptive significance. Then we use this knowledge to explain the design of, and interpret, an artificial selective harvest experiment. We evaluate the validity of *M. menidia* as a general model by extrapolation to and comparison with other species and fisheries. Finally, we argue that tractable biological models have an important place in fisheries science, particularly for difficult problems like teasing apart the genetic and environmental components of life history variation.

Seasonality and the evolution of countergradient growth variation in *M. menidia*

Like many marine fish species that inhabit nearshore waters along the east coast of North America, the Atlantic silverside has a broad latitudinal range, extending continuously from northern Florida to the Gulf of St. Lawrence. Its range crosses one of the steepest latitudinal temperature gradients in the world. Many elements of the ecology and life history of the Atlantic silverside are common to other marine species. *Menidia menidia* spawns in the spring in synchrony with full and new moons, releasing eggs of about 1 mm diameter that are broadcast with milt en masse by

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large schools of fish in the intertidal zone (Conover and Kynard 1984; Middaugh et al. 1984). Relative fecundity is exceedingly high, as batch spawning allows females to produce a cumulative egg mass roughly equivalent to their body mass over the breeding season (Conover 1985). Spawning occurs in salt marsh (*Spartina alterniflora*) environments that occur continuously along much of the North American east coast. Embryos attach to intertidal algae and *Spartina* without provision of postspawning parental care. Larvae hatch at about 5 mm in length and soon thereafter display schooling behavior that is maintained throughout life. Northern fishes migrate offshore to continental shelf waters in winter and return to the shore zone in spring (Conover and Murawski 1982). While it is possible that some degree of homing behavior may occur (this is currently being studied using otolith microchemistry), the species as a whole can essentially be thought of as a continuous distribution of subpopulations that can mix freely with nearest neighbors up and down the coast (Conover 1998, and see below). Where the life cycle of *M. menidia* departs greatly from that of other marine species is in age at maturity and longevity, which is 1 year for both traits throughout the species' range, although a few fish (generally <1%) reach age 2 at the northernmost latitudes (Conover and Ross 1982; Jessop 1983). Hence, silversides at all latitudes experience only one growing season before becoming an adult. This annual life cycle, and the ease with which it can be replicated in captivity, is what enables much of the research described below.

The Atlantic silverside provided the original discovery in fishes of temperature-dependent sex determination (TSD) (Conover and Kynard 1981). TSD is adaptive in *M. menidia* because it ensures that most fish produced at the beginning of the breeding season will become female, and it is female fitness that benefits more than male fitness from a longer growing season and thereby larger adult size (Conover 1984). To provide conclusive proof that TSD was adaptive, progeny from six locations representing different climates along the North American coast were reared at multiple identical temperatures. By standardizing the environment, such "common garden" experiments allow the genetic component of phenotypic differences among latitudes to be revealed. The results showed that the functional response of sex ratio to temperature differed greatly with latitude, proving that genetic adaptation existed (Conover and Heins 1987). Selection experiments on captive populations demonstrated that the functional relationship of sex ratio to temperature was capable of rapid evolution in response to climate change (Conover and Van Voorhees 1990). TSD is now known to occur in numerous species including commercially harvested and (or) cultivated species such as sockeye salmon (*Oncorhynchus nerka*), European sea bass (*Dicentrarchus labrax*), tilapia (*Oreochromis niloticus*), and several flatfishes (*Paralichthys* spp.) (Devlin and Nagahama 2002; Conover 2004). Only in the silverside, however, is the adaptive significance and evolvability of TSD understood, and this is principally because of the ease with which common garden experiments and selection experiments can be conducted with this species. Unexpectedly, these initial common garden experiments also provided evidence that many other characteristics of *M. menidia* differed genetically with latitude, especially those related to growth rate.

The Atlantic silverside displays a geographic pattern of variation in growth rate known as countergradient variation (CnGV) (Conover 1990; Conover and Present 1990). CnGV occurs when genotypes are distributed across an environmental gradient in nature such that genetic influences counteract environmental influences on a trait, thereby diminishing phenotypic variation (Conover and Schultz 1995). In the case of *M. menidia*, the capacity for growth (i.e., maximum rate expressed under unlimited rations) increases with latitude, thereby counteracting the decline in temperature and length of the growing season that would otherwise cause less growth in the north. The end result is that adult *M. menidia* are about the same size at all latitudes despite a threefold change in length of the growing season. Common garden experiments on progeny reared over multiple generations proved that the differences in growth rate are genetic (Conover and Present 1990). Because the genetic differences in growth are tightly correlated with latitude, they must be the result of selection rather than genetic drift.

What agents of selection might be responsible for CnGV in growth rate? A primary cause is the size dependency of winter mortality. Large fish survive the winter at higher rates than do smaller fish, and the severity and size dependence of winter mortality increase with latitude (Conover 1990; Schultz et al. 1998; Munch et al. 2003). Hence, with increasing latitude, the length of the growing season diminishes, while the necessity of large size increases, leading to increased selection for rapid growth in the north. But selection caused by winter mortality cannot be the complete explanation. Even in the absence of winter mortality, there are many other components of fitness that covary positively with size (e.g., fecundity, swimming performance, overall survival): why should low-latitude fish evolve submaximal rates of growth when higher rates are clearly possible? There must be trade-offs that cause balancing selection for submaximal growth.

To address this question, we investigated the physiological correlates of variation in growth rate. Northern genotypes grow faster by consuming more food and converting food more efficiently into somatic tissue while maintaining only a slightly higher routine metabolic rate (Present and Conover 1992; Billerbeck et al. 2000). Northern fish also store lipid reserves at higher concentrations prior to winter (Schultz and Conover 1997) and when spawning produce larger eggs at a higher rate with higher efficiency than do southern fish (Klahre 1998). Overall, bioenergetic model parameters for northern versus southern genotypes differed by an average of 28% (Munch and Conover 2002), clearly demonstrating the importance of accounting for intraspecific variation in physiology. In short, northern fish grow more rapidly than southern fish by adopting very high rates of energy acquisition and by allocating proportionately more of their acquired energy to tissue synthesis during the growing and spawning seasons.

Energy acquisition, digestion, and tissue synthesis are energetically expensive. In *M. menidia*, metabolic rate more than doubles after consuming a meal and is proportional to meal size (Billerbeck et al. 2000). Based on mass balance energy budgets, the trade-off with such high rates of investment in energy acquisition and tissue synthesis would likely involve activity. Recent experiments support this hypothesis.

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Northern fish are inferior to those from the south in terms of both sustained and burst swimming speed (Billerbeck et al. 2001). Experiments on growth-manipulated phenotypes within each genotype provided evidence that differences in swimming performance are a function of differences in growth rather than other intrinsic characteristics. Moreover, the cost of growth in terms of reduced swimming performance accelerates greatly as maximum growth rates are approached (Munch and Conover 2004). Hence, the marginal cost of growth can be reduced by not exceeding intermediate rates of growth.

For Atlantic silversides, schooling and fleeing when attacked are the principal means of evading predators. Thus, swimming performance should be directly linked to predator escape performance. This prediction was supported by experimental trials comparing predation rates of fast- versus slow-growing genotypes and growth-manipulated phenotypes (Lankford et al. 2001). Slow-growing fish are less susceptible to predators at a given size than are fast-growing fish when comparing either northern versus southern genotypes or growth-manipulated phenotypes within genotypes. In addition, the mere act of consuming large meals causes an immediate decline in swimming performance and an increase in predation vulnerability (Billerbeck et al. 2001; Lankford et al. 2001). Although these trade-offs have yet to be tested in the field (research currently in progress), there appear to be substantial costs associated with both the means (consuming large meals) and the end result (a bigger but relatively slower body) of rapid growth.

These studies of *M. menidia* suggest that growth rate and many of the underlying physiological traits that covary with and influence growth rate are fine-tuned to selection gradients that exist in nature. Size-dependent sources of natural mortality play a key role in explaining these gradients. Maintenance of such strong countergradient patterns in growth suggests both sufficient heritability within populations and ongoing selection. The former is a general prerequisite for evolutionary divergence and the latter is necessary to explain why gene flow, which appears to be substantial (Conover 1998), does not homogenize genetic variation along the coast. Individual physiological traits such as food consumption rate, growth efficiency, and metabolism are the foundation of stock productivity at the population level. If these traits are heritable and fine-tuned to size-dependent sources of natural selection in the wild, then there is every reason to suspect that such traits would evolve in response to artificial sources of size-dependent mortality that may be imposed by harvesting. We used selection experiments to address these issues.

Life history evolution under size-selective harvest regimes

We designed a size-selective harvest experiment with several questions in mind. First, what are the rates at which growth rate would evolve under size-selective harvest and how rapidly would such changes affect the productivity of populations? Second, what changes would occur in other traits correlated with growth rate and would these covary in a fashion similar to that of wild Atlantic silversides from different latitudes? Could artificial size selection alone create genotypes with physiologies like those of northern and southern fish in the wild? Finally, what would happen to populations that evolved in response to size-selective harvest and then experienced a selective harvest moratorium? Is it possible for evolution to reverse course back to the original condition and, if so, at what rate? The first two sets of questions will be discussed below, while the third is the subject of ongoing investigation.

The experiment involved the establishment of six captive populations of 1100 *M. menidia* collected from an intermediate latitude (New York) so that the intrinsic growth rate potential was in the middle of the range found in the wild (Conover and Munch 2002). Larvae were initially assigned randomly to each of the six populations so that the initial gene pools of the populations would be homogeneous. As the fish in each population reached adult size (i.e., day 190), 90% harvest rates were imposed. Two populations were harvested based on a minimum size rule (the largest 90% were harvested), two populations were harvested based on a maximum size rule (the smallest 90% were harvested), and two populations were harvested randomly with respect to size. The survivors (about 100 fish per population after accounting for incidental mortality prior to harvest) were induced to spawn, and their offspring were reared and treated as described above.

After only four generations of size-selective harvest, the yield of the populations had changed dramatically (Conover and Munch 2002). Yield in large size harvested lines was initially higher than the others but declined. The yield in small size harvested lines was initially low but increased. By the fourth generation of selection, the yield of small size harvested populations was twice that of large size harvested populations. The reasons for the yield differences were clearly due to genetic changes in the mean growth rate of fish within populations during both the larval and juvenile stages. Hence, gradients in size-dependent mortality are capable of causing rapid evolution of growth rate and thereby provide a plausible explanation for CnGV in the wild. These results also raise obvious concerns about the long-term effects of size-dependent harvest regimes on the productivity of populations.

Similarities in the physiology of the artificially selected fast- and slow-growing genotypes with those from different latitudes strengthen our conclusion that gradients in size-selective mortality account for countergradient growth variation in the wild. Walsh (2003) demonstrated that fish from lines that evolved faster growth also displayed significantly higher rates of food consumption and growth efficiency than those from slow-growing lines. Moreover, the fish from slow-growing lines displayed about a 10% faster critical swimming speed than fast-growing fish, although the differences were not significant and need further study before definitive conclusions can be drawn. Nonetheless, the changes in physiology caused by selective harvest are qualitatively similar to those existing at different latitudes in the wild. This suggests that our selective harvest experiment is a reasonably accurate mimic of selective agents operating in nature. It also shows that size-selective mortality alters a whole suite of interrelated physiological characters. If the potential for evolution of physiology in *M. menidia* can be generalized to other species, then the Darwinian response to

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harvest mortality clearly needs further attention by fisheries scientists.

Is *M. menidia* a valid model of general phenomena?

Our empirical simulation of the evolutionary effects of harvest has been criticized on the basis that harvest experiments on captive fish in controlled environments are not comparable with evolution in wild populations or in real fisheries. In the absence of knowledge about countergradient growth variation in the wild, this criticism would be highly appropriate, and there is always concern about the realism of any model, be it mathematical, statistical, or empirical. However, the harvest experiment was motivated specifically from detailed knowledge of natural variation in growth and its physiological correlates in response to a naturally occurring gradient in size-selective mortality. At least with respect to *M. menidia*, there appears little doubt that size-selective mortality in the wild exerts major influences on physiology and life history over contemporary time scales.

The question remains, however, whether or not the evolvability of life history traits and the magnitude of local adaptation are idiosyncratic in *M. menidia*. The rate at which a trait will evolve is a product of the heritability of phenotypic variation within a lineage or group (i.e., the proportion of phenotypic variance transmitted from parents to progeny) and the selection differential (i.e., the change in the trait mean that results from selection prior to reproduction) applied to that lineage. This fundamental identity of quantitative genetics is known as the breeder's equation. High heritability of traits coupled with large selection differentials would cause rapid evolution. Low heritability and moderate selection differentials would cause slow evolutionary change. Assuming at least moderate heritability, the potential for local adaptation in the wild is therefore determined by the change in selection differentials across environments. It is also influenced by the level of gene flow across environments. Large changes in the fitness of phenotypes combined with low gene flow across environments would lead to high levels of local adaptation. On the other hand, high gene flow across environments could swamp the effects of differential selection. If *M. menidia* is unusual in any of these characteristics, for example by displaying unusually high heritability for growth or fine-scaled spatial isolation of populations along the coast, then patterns observed in this taxon may not be general.

Available evidence would suggest, however, that these attributes in *M. menidia* are like those of numerous other marine species. The heritability for growth rate in *M. menidia* is about 0.2 (Conover and Munch 2002), a value similar to those observed for life history traits in many organisms including fishes (Roff 2002). Hence, the potential for evolution of growth-related traits within a population is not unusually high in *Menidia*. It should be pointed out that this heritability value applies strictly to the founders of the selection experiment, which were collected from New York. More northern or southern groups may have higher or lower growth rate heritability and therefore a different potential for evolution. Hence, at least for silversides from New York, the experiment demonstrates that there is sufficient genotypic variation in growth rate within extant populations to allow evolution, but not exceptionally so.

Menidia menidia is also not unique with respect to gene flow among populations. The level of gene flow is indexed by the geographic structure of genetic variation neutral to selection. High levels of genetic structure are found in species with highly isolated populations. Studies of population structure based on neutral molecular markers reveal that the proportion of total genetic variation attributed to populations in *Menidia* is low: i.e., on the order of about 1%–3% (Conover 1998), which is typical of marine species with dispersive life stages that lack barriers to gene flow. Hence, the evolvability and potential for local adaptation of physiological traits in *M. menidia* are not remarkable.

The annual life cycle of the Atlantic silverside is unique among temperate marine species of the western North Atlantic, and it belongs to a taxonomic family (Atherinidae) and order (Atheriniformes) in which relatively few long-lived, economically valuable species are found. Do the unique life history characteristics (nonoverlapping generations, lack of age structure) and taxonomic affinities of *M. menidia* limit its usefulness as a general model for fishes? The answer appears to be no. First, the existence of TSD, as first reported in *M. menidia*, has now been confirmed in numerous other species from many taxons and with highly divergent life histories, including over 50 fish species from 18 genera representing seven orders (reviewed in Devlin and Nagahama 2002; Conover 2004). Knowledge of TSD is crucial in development of methods for manipulating sex ratio in the aquaculture industry and in stock enhancement efforts where hatchery-reared fish are planted in the wild. Second, several long-lived, harvested species that inhabit eastern North America also appear to display CnGV in growth (Conover 1990). In striped bass (*Morone saxatilis*), for example, the parallels with *M. menidia* are clear. Striped bass sizes at the end of the first growing season are similar across latitudes (Conover 1990), size-dependent winter survival selects for larger young-of-the-year at northern latitudes (Hurst and Conover 1998), and experimental evidence from common garden experiments confirms that the capacity for growth increases with latitude (Conover et al. 1997). Evidence of CnGV in growth has also been found in numerous and phylogenetically diverse fishes including Atlantic halibut (*Hippoglossus hippoglossus*) (Jonassen et al. 2000), turbot (*Scophthalmus maximus*) (Imsland and Jonassen 2001), bay anchovy (*Anchoa mitchilli*) (Lapolla 2001), American shad (*Alosa sapidissima*) (Conover 1990), mummichog (*Fundulus heteroclitus*) (Schultz et al. 1996), and lake sturgeon (*Acipenser fulvescens*) (Power and McKinley 1997). In fact, CnGV in growth is so general that it has also been confirmed in insects (Gotthard et al. 1994; James and Partridge 1995; Arnett and Gotelli 1999), molluscs (Palmer 1994; Parsons 1997; Dittman et al. 1998), amphibians (Laugen et al. 2003), and reptiles (Ferguson and Talent 1993; Niewiarowski and Roosenberg 1993). Such findings demonstrate that adaptive genetic variation in physiological traits that underlay the production capacity of populations is widespread. Coupled with the knowledge from fish breeders that growth rate is also genetically variable within extant populations of many fishes, there appears to be little doubt that the production characteristics of wild populations are capable of evolving.

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It is obvious that our empirical simulation of the evolutionary response to harvest lacks realism in many ways. First is the extremely high and accurate size selection differentials that we imposed. Very few fisheries, if any, extract 90% of the population per year and do so with the size-selective accuracy that we enforced. Size-biased harvest in the wild will not exert selection on growth rate as directly as in our experiment and countervailing selection for increased growth may exist in nature, both of which would tend to slow the adaptive response. Second, *Menidia* populations consist of a single age-class that breed in synchrony with environmental cues and hence have non-overlapping generations. Such characteristics in other species would likely complicate the response to selection. For example, in stocks with variation in age at maturity, fishing mortality also tends to select for earlier size and age at maturity (Rijnsdorp 1993; Rochet 1998; Grift et al. 2003) and these traits likely display some level of either positive or negative coheritability with growth rate (see Munch et al. 2005). Hence, the combined effect of harvest selection on both growth rate and size and age at maturity cannot be deduced without knowing both the selection gradient imposed by the fishery and the genetic covariance of the traits in question. Information on these characteristics is not available for most fisheries. Third, we eliminated density dependence by standardizing recruitment each generation. However, had we allowed recruitment to proceed unchecked, the differences in yield among treatments would have been even greater owing to dramatic differences in reproductive potential that emerged among the harvested stocks. The important lesson from *M. menidia* is that evolutionary responses to natural and (or) anthropogenic size-selective mortality exist in nature, are dynamic properties of harvested populations, and hence must be better understood if natural genetic variability for life history traits and the production capacity of populations are to be conserved. Unfortunately, when it comes to predicting evolutionary responses in any particular fishery, the devil is in the stock-specific details of life history strategy, harvest selection gradients, and genetic variances and covariances. Detailed studies of model species could lead the way. We give two examples below.

First, data from model species can provide initial parameterization for population genetic models designed to probe evolutionary responses to harvest mortality. A prime example is the need to account for evolution of the variance–covariance matrix of correlated traits. As our *Menidia* experiments demonstrate, life histories represent a suite of correlated characters that respond in concert to various selective forces. Most studies of evolutionary response to harvest at best consider either growth rate or age at maturity, but in reality, these two traits likely have a genetic covariance that must be known to predict future changes. Such experiments will likely be possible only for a few species that will have to serve as models for others. Second, model species that can be easily cross-bred and reared in the laboratory are needed by molecular biologists to identify the actual genes that control life history. Eventually, molecular tools will allow us to track changes directly in wild populations at the gene level. In anticipation of such developments, depositories providing for routine preservation and storage of tissue samples from harvested populations should be instituted. In the future, such depositories will likely become as valuable to the study of evolutionary dynamics as catch-per-unit-effort has been to the study of population dynamics.

Conclusions

Despite the inherent difficulties, it is imperative that the evolutionary responses to harvest mortality begin to be addressed. Careful genetic analyses of rapid life history changes following introduction to novel environments are well established in several species (Reznick et al. 1997; Hendry et al. 2000; Quinn et al. 2001) and there is compelling new evidence of long-term changes in size at age (Sinclair et al. 2002; Haugen and Vollestad 2001) or age and size at maturity (Rijnsdorp 1993; Rochet 1998; Grift et al. 2003) in response to harvest in a variety of species. If the above still leaves doubt, consider also that in terrestrial systems, rigorous proof of rapid evolutionary change in response to size-selective hunting now confronts wildlife managers (Coltman et al. 2003). Unfortunately, when changes in response to harvest are genetic, they may be slow to reverse even when fishing stops because cessation of harvest mortality does not automatically ensure that natural agents of selection acting alone will exert sufficient pressure in the reverse direction. For example, Sinclair et al. (2002) showed that declines in size at age of Gulf of St. Lawrence Atlantic cod (*Gadus morhua*) during an intense period of fishing had not reversed in 10 years following a moratorium on harvest. The potential for near irreversibility of directional selection on body size and related traits underscores the need for precautionary approaches.

Fisheries scientists and managers may view dimly the existence of dynamic adaptive variation as just one more complication heaped upon an uncertain science. There are, however, several positive aspects. Knowledge of CnGV in growth, for example, can be used to help aquaculturists find genotypes in the wild with the fastest growth or other beneficial traits, and use of natural genetic variation avoids public disfavor with genetically engineered products. For example, Fontes (1998) showed that striped bass from Nova Scotia and New Brunswick grow much faster under intensive aquaculture conditions than do those from lower latitude stocks. Also, it is possible that harvest regimes might be developed for some wild fisheries that would select for faster rather than slower growth. Freshwater lakes offer an opportunity to test these ideas with replication in the field by using different harvest regimes, such as slot length versus minimum size rules, in multiple systems over several generations followed by common garden experiments (e.g., see an excellent example in Haugen and Vollestad 2001). Finally, the fact that wild populations are capable of rapid genetic adaptation is good news if persistence in the face of environmental change is the ultimate goal.

Empirical models like *M. menidia* play an important role in advancing our fundamental knowledge of fisheries science. Other examples of model species that have provided valuable insights and were studied despite minimal commercial value include bay anchovy and guppy (*Poecilia reticulata*). The broader disciplines of ecology and evolution have a long and successful history of using model species for advancing general knowledge (e.g., *Drosophila*,

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Tribolium, *Escherichia coli*, and *Arabidopsis*) and other biological disciplines focus almost all of their attention on a few model species (e.g., the zebrafish model in developmental biology). In fisheries science, we focus most of our attention on the species of greatest economic importance and, of course, this is necessary if we are to develop management plans for them. But all too often, these are the most difficult species to study empirically and hence, new fundamental discoveries come slowly. Species like *M. menidia* where all life stages are extremely easy to sample and study in the field, that have very simple life cycles and behavior, and that can be easily cultured in large captive populations over multiple generations in <1 year offer enormous advantages over most economically important species. Consider that both TSD and CnGV in *M. menidia* were discovered not from a priori theoretical predictions or from thoughtful foresight of the investigators but from incidental observations that were a by-product of studies designed for other purposes. It is the ease with which rigorous comparative field and laboratory observations could be conducted that enabled the findings described above. We argue that greater use of a model species approach will lead to future unforeseen discoveries that will increase our understanding of fish biology and fisheries science.

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Optimal life histories and food web position: linkages among somatic growth, reproductive investment, and mortality[1]

B.J. Shuter, N.P. Lester, J. LaRose, C.F. Purchase, K. Vascotto, G. Morgan, N.C. Collins, and P.A. Abrams

Abstract: Life history variation among 60 Ontario populations of lake trout (*Salvelinus namaycush*), walleye (*Sander vitreus*), cisco (*Coregonus artedii*), and yellow perch (*Perca flavescens*) is presented and interpreted using a biphasic model of individual growth that specifically accounts for the significant shift in energy allocation that accompanies sexual maturity. We show that the constraints imposed on life history variation by the character of the biphasic growth model are such that optimal life histories will exhibit associations among growth parameters, reproductive investment, and mortality that are largely consistent with associations evident in both our data set and earlier empirical studies; the von Bertalanffy growth parameter k varies with reproductive investment, and both k and investment vary with adult mortality. Our analysis suggests that within a food web, life history parameters will shift in a predictable fashion with the decreases in mortality expected as one moves from primary consumers up toward top predators. This expectation is supported by the differences in life history parameters that we observe between the two top predators in our data set (lake trout and walleye) and the two mid-trophic level consumers (cisco and yellow perch).

Résumé : Nous présentons les variations dans les cycles biologiques de 60 populations ontariennes de touladis (*Salvelinus namaycush*), de dorés (*Sander vitreus*), de ciscos de lac (*Coregonus artedii*) et de perchaudes (*Perca flavescens*) et les interprétons à l'aide d'un modèle biphasique de croissance individuelle qui tient compte spécifiquement du changement significatif d'allocation de l'énergie qui accompagne la maturité sexuelle. Nous démontrons que les contraintes imposées à la variation du cycle biologique par les caractéristiques du modèle de croissance biphasique sont telles que les cycles biologiques optimaux montrent des associations entre les paramètres de croissance, l'investissement reproductif et la mortalité qui sont en grande partie compatibles avec les associations présentes dans nos données et celles d'études empiriques antérieures: le paramètre de croissance de von Bertalanffy k varie en fonction de l'investissement reproductif et tant k que l'investissement varient en fonction de la mortalité des adultes. Notre analyse indique qu'à l'intérieur d'un réseau alimentaire, les paramètres démographiques vont se déplacer dans un sens prévisible en fonction du déclin de la mortalité attendu lorsqu'on passe des consommateurs primaires aux prédateurs supérieurs. Cette prédiction se réalise dans les différences observées dans les paramètres démographiques entre, d'une part, les deux prédateurs supérieurs (touladis, dorés) et, d'autre part, les deux consommateurs de niveau intermédiaire (ciscos, perchaudes).

[Traduit par la Rédaction]

Introduction

The von Bertalanffy growth model has been used by many authors as a vehicle for summarizing empirical variation in the life history of fish and for developing theory to account for that variation. This use continues in spite of strong criticism (e.g., Day and Taylor 1997) that the equation is, in principle, a flawed instrument that hides, within a fixed formal structure, the significant changes in energy allocation that characterize sexual maturation and that are the primary

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B.J. Shuter[2] and N.P. Lester. Department of Zoology, 25 Harbord Street, University of Toronto, Toronto, ON M5S 3G5, Canada, and Aquatic Research and Development Section, Ontario Ministry of Natural Resources, Peterborough, ON K9J 8M5, Canada.
J. LaRose, C.F. Purchase, and N.C. Collins. Department of Zoology, University of Toronto at Mississauga, Mississauga, ON L5L 1C6, Canada.
K. Vascotto and P.A. Abrams. Department of Zoology, 25 Harbord Street, University of Toronto, Toronto, ON M5S 3G5, Canada.
G. Morgan. Cooperative Fisheries Unit, Laurentian University, Sudbury, ON P3E 2C6, Canada.

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[2]Corresponding author (e-mail: shuter@zoo.utoronto.ca).

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subject matter of life history theory. Recently, more realistic models have been developed. Charnov et al. (2001) presented an analysis of life history variation based on a biphasic growth model that explicitly represents the consequences for somatic growth and future reproduction produced by the reallocation of energy to reproduction. Lester et al. (2004), in a related study, showed that a small set of empirically justifiable, simplifying assumptions was sufficient to develop a new model of lifetime somatic growth for fish, with the following useful attributes: (*i*) the lifetime growth pattern is biphasic, thus more accurately reflecting the shift in energy allocation that occurs with maturity; (*ii*) adult somatic growth is exactly represented by a von Bertalanffy growth equation with parameters that provide explicit information on the amount of energy allocated to reproduction; (*iii*) under the assumption that life histories are shaped by selection to maximize lifetime reproductive output, the model makes simple and explicit quantitative predictions of the relationships expected among age at maturity, reproductive investment, and total mortality that match observed relationships based on interspecific comparisons of freshwater fish.

In this paper, we use the biphasic model of Lester et al. (2004) to analyse an extensive new database that documents intraspecific variation in the life histories of four species of freshwater fishes: two species that typically fill the role of top predator (walleye (*Sander vitreus*) and lake trout (*Salvelinus namaycush*)) in their food webs and two species (cisco or lake herring (*Coregonus artedii*) and yellow perch (*Perca flavescens*)) that typically occupy a middle position in their respective food webs. We then assess the ability of the biphasic model to both describe and account for this variation. For each species, we proceed as follows: (*i*) we assess the validity of each of the primary simplifying assumptions that underpin the structure of the biphasic model; (*ii*) we assess the validity of the prediction that the parameters of the adult growth curve provide an indirect measure of reproductive investment; (*iii*) we assess the degree to which intra- and inter-specific variation in age at maturity, reproductive investment, and mortality follow the simple inter-relationships (Lester et al. 2004) generated by applying optimal life history theory to the biphasic model. Our analysis is restricted to female growth and reproductive investment, since for our four species, female investment in gonadal development is measurable and is likely to represent most of the reproductive investment made by individual females.

The biphasic von Bertalanffy growth model: a summary

When using the biphasic model to describe the somatic growth pattern typical of a particular population, we assume the following: (*i*) for all individuals, $W_s = aL^{3.0}$, where W_s is somatic weight (i.e., total weight less gonad weight), L is length, and a is a population-specific constant; (*ii*) for ages $t \geq T$, the age at which allocation of energy to reproduction begins, the surplus energy production by an individual of somatic weight W_s equals $(c_1 - c_2)W^{0.67}$, where c_1 is a constant defining the weight-specific rate of energy assimilation, and c_2 is a constant defining the weight-specific rate of energy expenditure on both maintenance and active metabolism; (*iii*) c_1 and c_2 can vary as a function of abiotic factors, such as temperature; (*iv*) for ages $t < T$, systematic changes in $(c_1 - c_2)$ can arise, depending on the character of the prey and predator fields experienced by the younger members of the population. Under these assumptions, potential somatic growth for age t fish (where t is in the neighbourhood of T) is given by

$$(1) \qquad L_t = h(t - t_1)$$

where L_t is length at age t, $h = (c_1 - c_2)/3a^{1/3}$, and the parameter t_1 captures, in a very simple fashion, the influence of both predator and prey fields on the early ($t << T$) growth of the focal organism: (*i*) $t_1 = 0$ if predators are absent and there are abundant prey species that vary widely in size so that the focal organism can shift smoothly from smaller to larger prey as it grows; (*ii*) $t_1 > 0$ if the presence of predators suppresses risky feeding behaviour (and therefore growth) in the focal organism until it grows beyond a critical size; (*iii*) $t_1 < 0$ if the prey field is truncated so that the availability of prey of suitable size does not keep pace with the increasing size of the growing focal organism, leading to a drop in somatic growth rate later in juvenile life. For females of age $t \geq T$, we assume: (*i*) investment of energy in reproduction begins in year T, and first spawning occurs a year later at age $T + 1$; (*ii*) $R = gW_s^{1.0}$, where R is the investment of energy in reproduction (i.e., eggs and gonadal tissue) by a typical mature female, measured in somatic wet weight units, and g is a population-specific constant; (*iii*) W_g, the wet weight of the mature female gonad at spawning, equals R/δ, where δ is the ratio of gonad energy density to soma energy density, on a wet weight basis. Under these assumptions, the realized somatic growth for a female aged $t > T$ is given by

$$(2) \qquad L_t = L_\infty[1 - e^{k(t - t_0)}]$$

where $L_\infty = 3h/g$, $k = \ln(1 + g/3)$, and $t_0 = T + \{\ln[1 - g(T - t_1)/3]/\ln(1 + g/3)\}$.

Next, we link investment in reproduction to fecundity (F) by assuming fecundity $F = W_g/W_e$, where W_e is the wet weight of a typical ripe egg and is assumed to be a species-specific constant. This permits us to use eq. 2 to calculate the lifetime reproductive output of a typical female given values for g and T. If we assume that differences in total adult mortality rate (Z) will select for T and g values that maximize the lifetime output of offspring by a typical female (e.g., Charlesworth 1994) and use the biphasic growth model to evaluate the consequences of such evolutionary effects, we generate the following predicted relationships among T, g, and Z:

$$(3) \qquad T \approx 1.95\frac{1}{e^Z - 1} + t_1$$

$$(4) \qquad g \approx 1.18\frac{e^Z - 1}{e^Z}$$

These functions are least squares fits to exact values obtained by numerical optimization (Lester et al. 2004). For Z in the range (0.05, 1.0), the difference between the exact value of T and the value given by eq. 3 is <0.3-year^{-1}, and the difference between the exact value of g and the value given by eq. 4 is <0.02-year^{-1}. These discrepancies are small relative to the changes in g and T expected (0.1–0.7 and 14–1, respectively), given a shift in Z from 0.05 to 1.0.

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Table 1. Summary of population life history statistics.

Character[a]	Species			
	Lake trout	Walleye	Cisco	Perch
h (cm·year^{-1})	5.4 (3.2, 9.0), n = 15	6.4 (3.5, 8.2), n = 18	4.0 (3.5, 6.0), n = 10	6.2 (4.2, 9.9), n = 17
T (year)	8.2 (5.9,11.1), n = 15	4.8 (3.6, 7.2), n = 18	3.4 (2.4, 4.1), n = 10	2.0 (1.1, 3.8), n = 17
L_T (cm)	47.0 (30.0, 65.1), n = 15	40.0 (31.1, 44.2), n = 18	23.4 (17.0, 30.3), n = 10	11.6 (6.1,16.5), n = 17
$L_{\infty\ (cm)}$	76.3 (52.2, 106.4), n = 15	85.8 (62.1, 123.5), n = 18	33.7 (23.5, 41.0), n = 10	34.9 (24.0, 46.6), n = 17
W_e (mg)	69.4	2.8	5.3	2.1
g (year^{-1})	0.21 (0.12, 0.30), n = 15	0.23 (0.14, 0.35), n = 18	0.40 (0.28, 0.50), n = 10	0.54 (0.29, 0.76), n = 17
Z (year^{-1})	0.22 (0.15, 0.30), n = 15	0.25 (0.17, 0.40), n = 18	0.38 (0.23, 0.55), n = 10	0.55 (0.34, 0.73), n = 15

Note: Data are mean, range (in parentheses), and number of populations. Egg weights for lake trout, cisco, and perch were derived as follows: egg volume was calculated from egg diameter and converted to weight, assuming a specific gravity of 1.0. Sources for egg diameter estimates for each species areas follows: lake trout, 5.1 mm (direct measurement of ripe eggs from two populations, mean of several population values in Martin and Olver 1980); cisco, 2.1 mm (mean of values in Brooke (1970), Henault and Fortin (1991), Scott and Crossman (1973)); perch, 1.5 mm (Craig (2000)). The egg weight for walleye was derived from dry weight values given in Johnston and Leggett (2002) and converted to wet weight assuming a conversion factor of 3.15. All populations are found within the region bounded by 43°N–53°N latitude and 75°W–95°W longitude.

[a] h, potential somatic growth rate just prior to age T; T, age at which allocation to reproduction begins; L_T, fork length at age T; L_∞, maximum female size; W_e, egg wet weight; g, annual investment in reproduction by a mature female; Z, instantaneous mortality rate suffered by mature females.

The following is a brief summary of the parameters that we use in this paper (Table 1): T (years), age at which allocation to reproduction begins; $T + 1$ (years), age of first spawning; h (cm·year^{-1}), potential somatic growth rate just prior to age T; L_T (cm), fork length at age T; L_∞ (cm), maximum female size, estimated by fitting a von Bertalanffy curve to the growth pattern of mature females; W_e (mg), egg wet weight; g (year^{-1}), annual investment in reproduction by a mature female, measured as the proportion of her somatic weight that is energetically equivalent to her investment in eggs, gonadal tissue, and reproductive behaviours; Z (year^{-1}), instantaneous mortality rate suffered by mature females.

Methods

Field sampling

Sampling for walleye, perch, and cisco was carried out in the fall of the years from 2000 through 2002 as part of a survey program sponsored by the Ontario Ministry of Natural Resources. Multipaneled sinking gill nets with mesh sizes ranging from 25 to 152 mm were randomly set throughout the lakes at depth strata of 2–5 m and 5–15 m. Additional samples were obtained from a few populations using similar methods by university researchers. Fish were measured for fork length and round weight. A subsample of the catch was assessed for sex and maturity. Gonads were weighed and preserved in ethanol for later determination of fecundity. Fecundity was estimated by counting all of the eggs in a weighed subsample (~10% of total gonad weight) of tissue taken from the centre of the gonad. Ages were determined from otoliths.

Sampling for lake trout was carried out in the spring and summer of years 1980 to 2002, under a variety of survey programs sponsored by Ontario Ministry of Natural Resources (Shuter et al. 1998; Payne et al. 1990). Gear and sampling protocols varied among populations (i.e., methods used included gill and trap net surveys and creel surveys) but were always designed to give a representative sample of both mature fish and older immature fish. Sampling for fecundity was rarely done. Fall sampling of spawning fish in two lakes (Louisa and Opeongo) was carried out to obtain more extensive estimates of egg size and fecundity. This was supplemented with values reported by Trippel (1993) and Peck (1986). Growth and maturity data from the long-term lake trout monitoring program on Lake Opeongo (see Shuter et al. 1987 for study details) were also included in this analysis.

Estimating individual characteristics

Sex was determined by internal examination of gonads. Categorization of female maturation was based on the presence of developing eggs. Total potential fecundity (F) was estimated by counting the number of eggs in a weighed sample of gonad tissue to estimate eggs per gram, and then multiplying this estimate by the total gonad weight for the animal. For lake trout, walleye, and perch, the weight of the female gonad at spawning was calculated as

$$W_g = FW_e$$

where W_e is the average wet weight of a ripe egg (Table 1). Egg weights for lake trout, cisco, and yellow perch were calculated from egg diameters, assuming a spherical shape and a specific gravity of 1.0. In the absence of direct measurements for each species, this is a reasonable approximation given Kamler's (1992) compendium of data on fish egg composition. Her data demonstrates that a typical egg is 61% water, 26% protein, and 7.5% lipid. The remaining 5% is a mixture of carbohydrate and ash. The estimated specific gravity of such an egg is 1.05, assuming the water, protein, and lipid proportions listed above, plus specific gravity values of 1.0, 1.2, and 0.95 (Lehninger 1970) for water, protein, and lipid, respectively. Walleye egg weight was taken directly from dry weight values reported in Johnston and Leggett (2002). For cisco, fecundity was estimated for only a small subset (six) of all the populations in the study, but gonad weights were recorded for all populations at about 4–6 weeks prior to spawning. These values were used to estimate fecundity by dividing them by the average number of eggs (538) per gram of gonad tissue determined from the six populations with fecundity estimates. Ripe gonad weight was then estimated from this fecundity estimate by multiplying by the W_e value for cisco (Table 1). For all species, re-

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Table 2. Exponent estimates in the critical allometric relationships for each species.

Species	Somatic weight ∝ (fork length)^b	Fecundity ∝ (somatic weight)^c
Lake trout	3.20 (3.05, 3.36), n = 12	1.17 (0.69, 1.57), n = 8
Walleye	3.13 (2.96, 3.42), n = 22	1.10 (0.88, 1.75), n = 22
Cisco	3.05 (2.82, 3.36), n = 18	0.90 (0.80, 0.99), n = 4
Perch	3.16 (2.88, 3.31), n = 20	1.05 (0.87, 1.20), n = 20

Note: Data are mean, range (in parentheses), and number of populations (e.g., mean b value for lake trout = 3.20; mean c value = 1.17).

productive investment was estimated from ripe gonad weight by multiplying by a conversion factor (δ) to correct for energy density differences between eggs and somatic tissue. For perch and walleye, values for this energy conversion factor were 1.24 (derived from data in Henderson et al. (2000)) and 1.41 (from Henderson and Nepszy (1994)), respectively. For lake trout and cisco, values were 1.52 (from Jonsson et al. (1991)) and 1.75 (from Lahti and Muje (1991)), respectively. The latter three values all fall close to the median value (1.6) reported by Gunderson and Dygert (1988) in their review of reproductive investment in marine species. Egg–soma energy density ratios based on wet weights will generally be significantly larger than energy density ratios based on dry weights, because fish egg tissue tends to have a lower water content than fish soma tissue. For example, in Kamler's (1992) summary of egg composition data, the water content of a typical egg is 61% compared with 82% for soma.

Estimating population characteristics

Logistic regression (StatSoft 1994) was used to estimate the relationships linking the fraction of mature females to age and to length. These relationships were then used to estimate both the age (T) and length (L_T) at which females begin to allocate energy to reproduction. Adult mortality was estimated from the maximum observed age of fish in each population using Hoenig's (1983) empirical formula: $Z = 4.22(\text{maximum observed age})^{-0.982}$. The lifetime growth pattern for each population was characterized as follows. The prematuration somatic growth rate was estimated using standard linear regression on the length-at-age data for immature fish. Changes in net production during the pre- and immediate post-maturation periods were assessed by examining somatic growth rates of immature fish prior to, and just after, the population age at maturity. Significant systematic shifts in prematuration growth rate were reflected by non-zero t_1 values. The postmaturation growth curve was estimated using nonlinear regression to fit eq. 2 to length-at-age data for ages $t \geq T$. The fit provided by eq. 2 depends on four parameters: h, t_1, T, and g. We searched for the value of g that would best describe the growth of mature females, given a value for T based on the maturation schedule and values for h and t_1 based on the growth of immature fish in the neighbourhood of T.

Results

We described growth characteristics of 15 lake trout, 18 walleye, 10 cisco and 17 yellow perch populations (Table 1). All 60 populations are spread across the relatively large geographic area of Ontario (Table 1). Intraspecific variation for many population characteristics is quite large and the interspecific variation is even larger.

Are the assumptions regarding size-dependence met?

The biphasic model makes several assumptions regarding the length-dependence of somatic weight and the somatic weight-dependence of both mature gonad weight and fecundity. These relationships were evaluated for each population (Table 2), and we found that (*i*) for all four species, the assumption that weight varies as the cube of length was closely adhered to; and (*ii*) the assumption that fecundity varies with somatic weight was closely adhered to, and hence the assumption that mature gonad weight varies with somatic weight was met, given fixed ripe egg size.

Does the biphasic growth model provide a good description of lifetime growth pattern?

The biphasic model successfully described the range of growth patterns seen in the four species of fish (Fig. 1). The examples shown clearly demonstrate a switch from linear to asymptotic growth at the age of maturity. For lake trout, walleye, and cisco, somatic growth rate during the first year of life usually exceeded the average somatic growth rate for the rest of the prematuration period. Because the growth rate just prior to maturity was relatively constant (Fig. 1), this aspect of the prematurity growth pattern was adequately captured by including estimated t_1 values that were significantly less than 0 (see Lester et al. 2004 for details). For yellow perch, growth rate from birth to maturity was relatively constant, and thus we could set t_1 to zero for all populations.

Does adult growth reflect reproductive investment?

Given that g values estimated from the lifetime growth pattern should reflect relative investment averaged over the entire reproductive life cycle, we characterized the reproductive investment typical for each population as the value of W_g/W_s for a female midway through her reproductive lifespan and characterized by a length $L_{mid} = (L_T + L_\infty)/2$, where L_T and L_∞ are population-specific values. Values for W_g and W_s were estimated from L_{mid} using population-specific weight and fecundity regression relationships. We then compared this direct estimate of reproductive investment with our g estimate derived from the growth pattern of mature females (Fig. 2).

Within species, the median values and ranges for our direct and indirect estimates of reproductive investment were very similar (Table 3). We found significant positive associations between our direct measure of reproductive investment and the estimates of g derived from the lifetime somatic growth pattern for walleye (Spearman's $R = 0.65$, one-sided $p < 0.003$) and for perch (Spearman's $R = 0.48$, one-sided

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Fig. 1. Sample prereproductive (open circles, observed values; broken line, fitted relationship) and postreproductive (solid circles, observed values; solid line, fitted relationship) growth patterns for (*a*) lake trout (*Salvelinus namaycush*, Squeers Lake), (*b*) walleye (*Sander vitreus*, Wakami Lake), (*c*) lake herring (*Coregonus artedii*, Red Cedar Lake), and (*d*) yellow perch (*Perca flavescens*, Nagagamisis Lake). The two fitted relationships, which characterize each phase of the overall growth trajectory, have been drawn over a broad range of ages to emphasize the contrast between the phases. Fitted values for h (prereproductive somatic growth rate) and g (reproductive investment) are given for each curve.

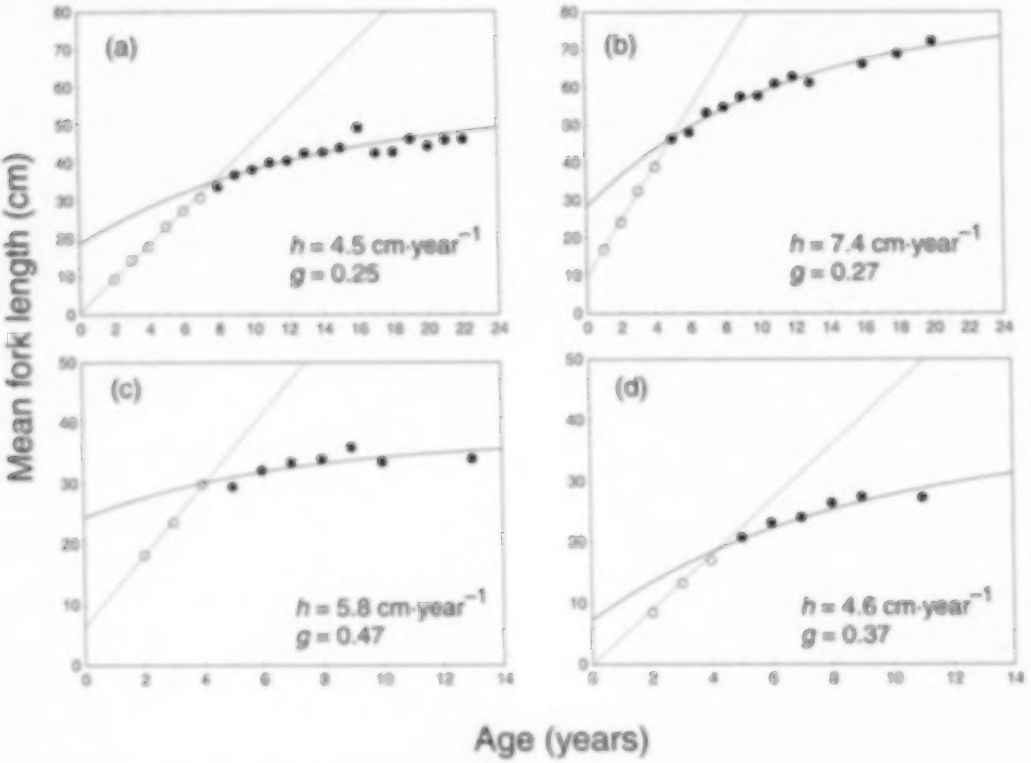
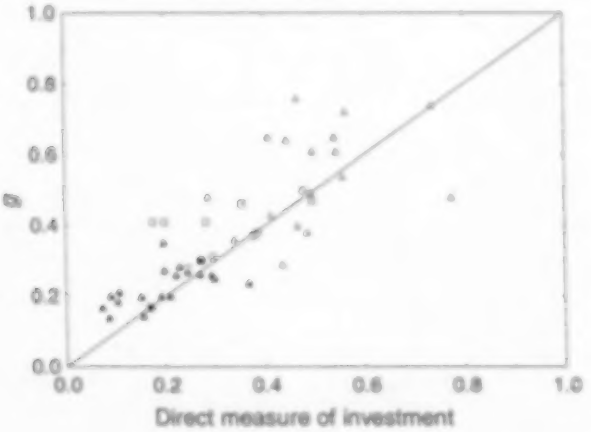


Fig. 2. Comparison between direct estimates of reproductive investment, based on measured female gonad weight, and indirect estimates of reproductive investment, obtained by estimating g from a von Bertalanffy fit to the somatic growth trajectory of mature females. The solid line is the 1:1 line. Lake trout (*Salvelinus namaycush*), solid squares; cisco (*Coregonus artedii*), open squares; yellow perch (*Perca flavescens*), open triangles; walleye (*Sander vitreus*), solid triangles.



$p < 0.04$). There were not enough populations in the lake trout data set to permit a meaningful assessment of association. For cisco, the association between the two measures was not statistically significant (Spearman's $R = 0.08$).

Are reproduction and adult mortality linked as predicted by life history theory?

Observed variation in T, g, and Z for each of our four species is summarized (Table 1 and Fig. 3). Intraspecific variation for most parameters is relatively high, with the maximum observed value typically 2–3 times the minimum observed value. Total mortality values are higher for the mid-trophic-level species. T and g estimates appear to vary with total mortality in accordance with eqs. 3 and 4 (Fig. 3).

Discussion

For the four species in this study, the primary assumptions that underlie the biphasic growth model are largely met, and the model is capable of providing a good description of observed lifetime growth patterns. For long-lived species with relatively late maturation ages (e.g., lake trout), the biphasic character of the growth pattern is clearly demonstrated. The fact that growth-based g values are similar to direct measures of reproductive investment supports the premise that

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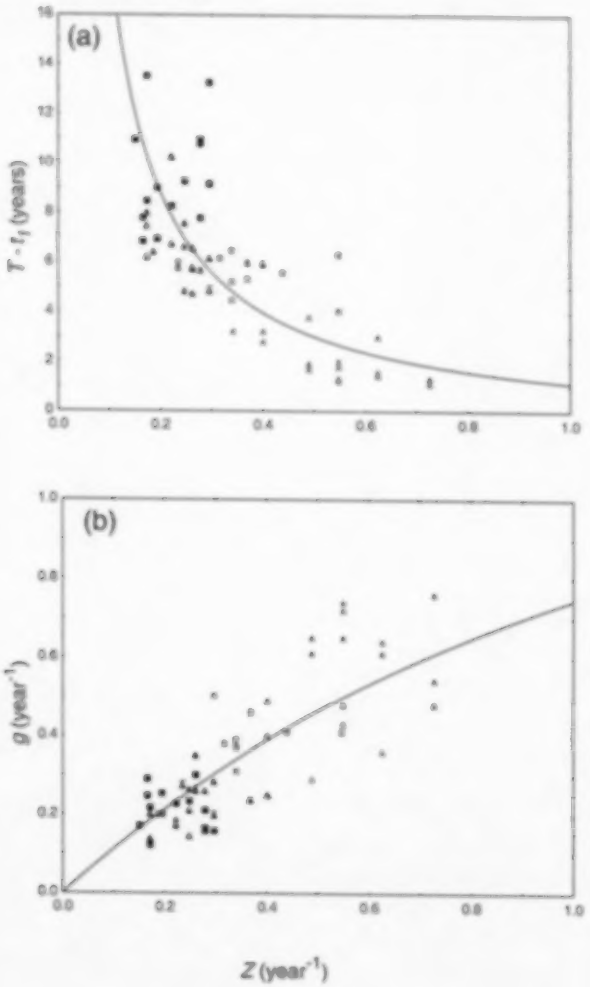
Table 3. Comparison of direct and indirect estimates of reproductive investment.

Species	Measure of investment	
	Direct	Indirect
Lake trout	0.21, (0.18–0.22), $n = 2$	0.21, (0.12–0.30), $n = 15$
Walleye	0.24, (0.09–0.44), $n = 18$	0.22, (0.14–0.35), $n = 18$
Cisco	0.32, (0.17–0.48), $n = 10$	0.41, (0.16–0.55), $n = 10$
Perch	0.49, (0.29–0.78), $n = 17$	0.54, (0.29–0.76), $n = 17$

Note: Data are median, range (in parentheses), and number of populations. Direct estimates of investment were derived from measurements of gonadal development in mature females; indirect estimates were obtained from fitting the biphasic growth curve to length-at-age data from mature females.

Fig. 3. Comparison between observed and predicted values for ($T - t_1$) and reproductive investment (g). Each point represents the observed values for a particular population. The solid lines are the predicted values derived from eqs. 3 and 4, respectively. Z is total adult mortality rate. Lake trout (*Salvelinus namaycush*), solid squares; cisco (*Coregonus artedi*), open squares; yellow perch (*Perca flavescens*), open triangles; walleye (*Sander vitreus*), solid triangles.



female adult growth pattern is shaped by reproductive investment. For all four species, the median values for both the direct and indirect measures of reproductive investment were similar; however, only two of the three intraspecific comparisons exhibited statistically significant positive associations between these two measures. The weakness of these intraspecific associations may stem from the fact that population data (rather than individual data) were used to derive each of the measures — the growth trajectory-based g values came from mean length-at-age data and the direct measures of reproductive investment came from mean fecundity – somatic weight data. These data averaged over cohorts, were frequently based on different subsamples of fish, and thus may only loosely reflect the close connection between somatic growth and reproduction that is assumed to exist for individuals, as represented in the biphasic growth model. This suggests that a more exacting test of this model should be based on growth and reproductive investment data derived concurrently from the same individuals.

Since the observed associations among T, g, and Z match the relationships predicted by applying simple life history theory to the biphasic growth model, we conclude that a significant portion of the demographic variation exhibited among populations of these four species can be attributed to the shaping of life histories to match ambient mortality rates by some combination of selection and phenotypic plasticity. For mid-trophic-level species (cisco and perch), these ambient mortality rates are natural rates in the sense that they do not contain a component that is driven directly by human activities, such as fishing. For the top predators (lake trout and walleye), the ambient rates do contain a fishing component. However, the populations in our data set have been subjected to moderate levels of fishing for several generations and, as is evident from other papers in this symposium (e.g., Munch et al. 2005; Olsen et al. 2005; Reznick and Ghalambor 2005), selection imposed by fishing can operate rather quickly to alter the reproductive characters of adults. Thus, it is at least possible that selection may be the primary force underlying the correspondence between observed and predicted values of T and g shown in this study.

In our earlier paper (Lester et al. 2004), we showed that these predicted associations among T, g, and Z were also consistent with patterns of interspecific demographic variation evident in a large sample of North American freshwater fish. If we assume that this theory has some validity for fish generally, then it provides a simple, mechanistic account of the frequently observed empirical association between the parameters of the von Bertalanffy growth curve and mortality (e.g., Beverton 1963; Pauly 1980; Charnov 1993) and

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Table 4. Comparison of observed and predicted values for the quantities identified by Charnov (1993) as life history invariants.

Quantity	Nominal value or range cited in Charnov (1993)	Predicted value*
$(T + 1)Z$	(1.75, 2.20)	(1.95, 2.10)
L_{T+1}/L_∞	0.65	(0.42, 0.73)
Z/k	(1.65, 2.10)	(2.6, 4.5)
$\phi^\dagger$	(–0.8, –0.4)	–1

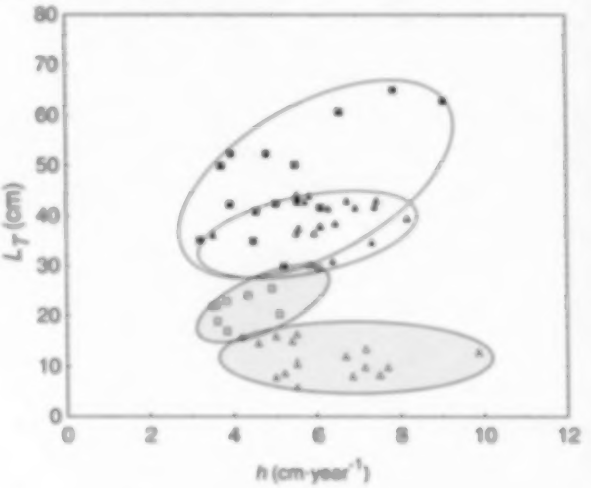
*Predicted values are generated from applying eqs. 3 and 4 to the biphasic growth model for a range of Z values from 0.05 to 1.0.
†$\ln L_\infty = k^\phi$.

also of the empirical association between direct measures of reproductive investment (e.g., female gonadosomatic index) and mortality (Gunderson and Dygert 1988; Gunderson 1997). Optimization of demographic characters that are constrained by the biphasic growth model "naturally" produces associations among growth parameters, reproductive investment, and mortality, which are largely consistent with the empirical associations documented in these earlier studies. Fits of the von Bertalanffy equation ($L_t = L_\infty[1 - e^{k(t-t_0)}]$) to observed adult growth patterns yield values for k that vary with reproductive investment (since $k = \ln(1+g/3)$), and reproductive investment (as measured directly through the gonadosomatic index or indirectly through k) will vary with mortality (see eq. 4).

Charnov (1993) summarized various empirical associations among life history parameters and mortality in terms of four quantities that he termed "life history invariants" — dimensionless quantities that appeared to be relatively constant when estimated for a variety of species, living under a wide range of environmental conditions (Table 4). Our theoretical analysis of life history variation yields predictions for these quantities that can be compared with Charnov's summary (his Chapter 4, our Table 4).

Our analysis predicts that the first quantity ($(T + 1)Z$) is essentially invariant under a wide range of mortality rates, with a value very similar to that given by Charnov (1993). The second quantity (L_{T+1}/L_∞) varies with mortality, but the range of variation is less than twofold for mortality rates between 0.05 and 1.0, and Charnov's nominal value sits close to the middle of that range. However, our analysis, unlike Charnov's, predicts a systematic decline in L_{T+1}/L_∞ with increasing mortality. Our predictions for the third (Z/k) invariant differ somewhat from Charnov's summary. Our analysis predicts that Z/k will increase with mortality, giving a range of values that is just above the range cited by Charnov as "typical", but is well within the overall range defined by the Pauly (1980) data set (0.60 to 4.6 is the 90% range), which was Charnov's primary source. This discrepancy could stem in part from a systematic bias in the estimate of k that can arise when a single von Bertalanffy equation is used to describe the entire lifetime growth trajectory. We simulated this situation (B.J. Shuter, unpublished data) by using a nonlinear least squares (S-Plus 2001) procedure to fit a single von Bertalanffy function ($L_T = L_\infty(1 - e^{-kt})$) to the optimal (as specified by eqs. 3 and 4) biphasic growth curves for Z values ranging from 0.1 to 1.0. We found that the least squares estimate of k was always higher than the true value, with the ratio of the biased to the true value declining from 1.5 toward 1.0 as Z increased from 0.1 to 1.0. When we substituted this biased estimate of k for the true value in Charnov's third invariant (Z/k) we found very similar values (1.78, 2.8) to those cited as "typical" by Charnov for $Z \in (0.1, 0.5)$ and somewhat larger values (3.1, 4.1) for $Z \in (0.6, 1.0)$.

Fig. 4. Observed values for length at maturity (L_T) and pre-reproductive somatic growth rate (h). Values for each species have been enclosed with an ellipse. The ellipses for the two mid-trophic-level species have been shaded to distinguish them from the two top predators. Lake trout (*Salvelinus namaycush*), solid squares; cisco (*Coregonus artedii*), open squares; yellow perch (*Perca flavescens*), open triangles; walleye (*Sander vitreus*), solid triangles.



Our model predicts that the fourth quantity (ϕ in $L_\infty \propto k^\phi$) should be truly invariant with a value (–1) that is just below the range (–0.8 to –0.4) cited by Charnov as typical. The positive bias in k estimates mentioned above cannot account for this discrepancy; however, one factor that might be responsible is density-dependent plasticity in growth. This effect is omitted from our model and from Charnov' models (Charnov 1993; Charnov et al. 2001). In our model, $L_\infty = 3h/g$ and $k = \ln(1 + g/3)$. This implies that L_∞ is approximately proportional to hk^{-1}, and thus the relationship between L_∞ and k will be affected by systematic changes in growth rate (h). The increase in ϕ comes about if we assume that higher Z, and consequently higher k values, are associated with relatively low-density populations, where typical adults enjoy higher surplus energy production and hence higher h values. The rate of decline in L_∞ with increasing k, which is inherent in our basic model, would be ameliorated by this effect, resulting in an estimate for ϕ that is greater than –1 and therefore closer to the typical range cited by Charnov (Table 4). Trends in our data are consistent with the existence of this effect; within each species, growth rate was positively related to reproductive investment.

Given that the theoretical predictions summarized in eqs. 3 and 4 have some general validity, we would expect that within a food web, life history parameters will shift in a predictable fashion with the decreases in mortality expected as one moves from primary consumers up toward top preda-

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tors. This expectation is born out by the observed differences in both mortality and life history characteristics between our two mid-trophic-level consumers and our two top predators. The top predator species mature at older ages and larger sizes, invest less in reproduction, and attain larger asymptotic sizes. The observed differences in g and T are expected, given that mortality rates are lower for top predator species. In the following arguments, we show that larger L_∞ and L_T (Fig. 4) values among the top predators can also be interpreted as consequences of smaller g and Z values. According to the biphasic growth model, $L_\infty = 3h/g$ and thus variation in L_∞ is potentially explained by variation in prematuration somatic growth rate (h) and (or) reproductive investment (g). With our four species, the prematuration growth rates of mid-trophic-level species and top predator are very similar (Fig. 4), while the g values for top predators are roughly half the g values for mid-trophic-level species. Thus, the higher L_∞ values among the top predators are explained mainly by the lower investment in reproduction associated with lower mortality rates. Similarly, the higher sizes at maturity (L_T) among top predators (Fig. 4) can also be interpreted as a consequence of lower mortality rates. Given (*i*) that L_T varies with hT (eq. 1), (*ii*) that T is given by eq. 3, then L_T will vary with $h/(e^Z - 1)$, and (*iii*) since values of h are independent of trophic position but values of Z decline with increasing trophic position, then increases in L_T with increases in trophic position are expected and are observed (Fig. 4).

Our results suggest that in an unexploited food web, the life histories of the resident fish species will be shaped by the progressive decline in adult mortality that accompanies the relaxation of predation pressure experienced by primary, secondary, and tertiary consumers. This set of interdependent mortality rates will have shaped the life histories of the fish in the web and thus will have determined, to a significant degree, their responses to increasing rates of exploitation. When directed exploitation raises the mortality rate for one species, it will produce a cascade of changes in the mortality rates experienced by species at successive trophic levels below that of the harvested species. Over time, these changes will promote the evolution of a new suite of life history traits among the fish species of the web, with a variety of consequences for their population dynamics. Raising fishing mortality rates to levels that are high relative to the natural rates for the exploited species in the web will exaggerate both the magnitude and extent of this cascade, with consequences that are currently unpredictable and possibly undesirable.

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Integrating the effects of fish exploitation and interspecific competition into current life history theories: an example with lacustrine brook trout (*Salvelinus fontinalis*) populations[1]

Pierre Magnan, Raphaël Proulx, and Michel Plante

Abstract: We used data from 17 populations of lacustrine brook trout (*Salvelinus fontinalis*) of the Canadian Shield, southern Quebec, to test whether early maturity (in males and females) and high reproductive effort (in females) are associated with increased (*i*) fish exploitation (sportfishing) and (*ii*) interspecific competition through their effects on growth and survival. The age at maturity of males and females was inversely related to the intensity of both fishing and interspecific competition. Fishing and interspecific competition affect the age at maturity through their effect on adult survival but not on growth, supporting predictions of life history models based on survival. In contrast, we did not find consistent effects of interspecific competition and fishing on the gonadosomatic index of females, which was directly related to survival (in all populations) and to the age at maturity (in exploited populations). These latter results are contrary to the predictions of life history models under the assumption that survival is directly related to growth rate. Our results suggest that reproductive effort and age at maturity are not dependent on growth when survival is independent of growth, as is the case in exploited and sympatric populations experiencing low adult survival but high growth.

Résumé : Nous avons utilisé les données de 17 populations lacustres d'omble de fontaine (*Salvelinus fontinalis*) du bouclier canadien, du sud du Québec, pour tester l'hypothèse qu'une maturité précoce (chez les mâles et les femelles) et un effort reproducteur élevé (chez les femelles) sont associés à une augmentation de (*i*) l'exploitation par la pêche sportive et (*ii*) la compétition interspécifique via leurs effets sur la croissance et la survie. L'âge à maturité des mâles et des femelles était inversement relié à l'intensité de la pêche et de la compétition interspécifique. La pêche et la compétition interspécifique ont affecté l'âge à maturité par leurs effets sur la survie des adultes mais non sur la croissance, supportant les prédictions des modèles de stratégies de vie basés sur la survie. Par contre, nous n'avons pas trouvé d'effets cohérents de la compétition interspécifique et de la pêche sur l'indice gonado-somatique des femelles, lequel était directement relié à la survie (pour toutes les populations) et l'âge à maturité (pour les populations exploitées). Ces derniers résultats sont contraires aux prédictions des modèles de stratégies de vie qui assument que la survie est directement reliée à la croissance. Nos résultats suggèrent que l'effort reproducteur et l'âge à maturité ne sont pas dépendants de la croissance lorsque la survie est indépendante de la croissance, comme c'est le cas des populations sympatriques et exploitées par la pêche, dont la survie des adultes est faible mais la croissance élevée.

Introduction

Current life history theories suggest that the reproductive investment and age at maturity of animals vary in response to age-specific survival rates if the expectation of producing future offspring is a selected trait (Schaffer 1974; Stearns 1976; Hutchings 1993). In this context, an individual should trade off between present fecundity and future survival if one assumes that age-specific fecundity does not change with age-specific survival (Charlesworth 1980; Hutchings 1993). Growth is also expected to be involved in this trade-off because of its direct influence on age-specific fecundity (Schaffer 1974; Hutchings 1993). This is especially true for species with indeterminate growth like fish, where fecundity is positively related to body size (Kozlowski and Uchmanski 1987). Growth rate could also be indirectly re-

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P. Magnan[2] and R. Proulx. Groupe de recherche sur les écosystèmes aquatiques, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, QC G9A 5H7, Canada.
M. Plante. Parc national du Canada de la Mauricie, Parcs Canada, 2141, Chemin Saint-Paul, Saint-Mathieu du Parc, QC G0X 2V0, Canada.

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[2]Corresponding author (e-mail: pierre_magnan@uqtr.ca).

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lated to environmental factors associated with mortality and thus act as a signal to individuals about impending mortality (Stearns and Koella 1986). Different mathematical models have been suggested to predict the variations in reproductive effort and age at maturity from an organism's growth and survival (Roff 1984; Stearns and Koella 1986; Hutchings 1993). These models predict that high adult survival favours low reproductive effort and delayed reproduction, whereas increased juvenile growth rate favours high reproductive effort and early reproduction. The models of Roff (1984) and Stearns and Koella (1986) do not distinguish juvenile from adult growth rates, whereas that of Hutchings (1993) considers that the ratio of juvenile to adult growth is more significant than growth rate per se when predicting life history strategies.

Direct empirical support of the above theoretical predictions was provided by Hutchings (1993), who found that high juvenile to adult growth and survival ratios were associated with high reproductive effort and early maturity in three populations of unexploited brook trout (*Salvelinus fontinalis*) inhabiting small streams. Fox and Keast (1991) found that pumpkinseed (*Lepomis gibbosus*) populations experiencing high overwinter mortality exhibited earlier maturity and higher reproductive investment than populations in low-mortality environments. Fox (1994) also found that large and fast-growing juveniles, and to some extent high juvenile to adult growth ratios, favoured early maturity and high gonadal investment in a study of 27 populations of lacustrine pumpkinseed. In a metaanalysis of 85 marine and freshwater fish species, He and Stewart (2001) found a nonlinear negative relationship between the von Bertalanffy growth coefficient (K) and the age at first reproduction ($T - t$). These predictions were also indirectly supported by studies relating potential for growth and survival to geographical gradients and environmental factors (Leggett and Carscadden 1978; Fleming and Gross 1990; Duchesne and Magnan 1997).

Few studies have been designed to explicitly test the effects of both competition and fish exploitation on variations of life history traits of a species in the same system. Growth and survival appear to be the driving factors that explain variations in reproductive effort and age at maturity. It is thus important to first understand the effects of exploitation and competition on growth and mortality before predicting their effects on reproductive effort and age at maturity. Based on current fishery theories, fish exploitation has a direct negative impact on adult survival (Jennings and Kaiser 1998; Hall 1999; Rochet et al. 2000). The effect of fishing on growth is more difficult to predict. Sustained removal of larger and fast-growing animals will select for small-sized, slow-growing individuals (Rochet et al. 2000). On the other hand, harvesting may release populations from density regulation, and consequently, individuals can undergo growth compensation as the intraspecific competition declines (Jennings and Kaiser 1998; Hall 1999; Rochet et al. 2000). So, the growth trajectory will depend on the species' intrinsic potential for growth (i.e., slow- versus fast-growing species) and the fishing intensity. Regarding interspecific competition, it has been shown that survival and growth of juvenile pumpkinseed are reduced in the presence of bluegills (*Lepomis macrochirus*) (Mittelbach 1988; Osenberg et al. 1992). Persson and Greenberg (1990) also observed a reduction in growth of age-0+ and age-1+ perch (*Perca fluviatilis*) with increasing roach (*Rutilus rutilus*) density in an enclosure experiment. However, as for fishing, increased mortality associated with competition could also involve growth compensation through a decrease in intraspecific competition. Thus, one can predict that fish exploitation and interspecific competition will promote high reproductive effort and early reproduction through their negative effect on survival. However, fish exploitation and interspecific competition will affect reproductive effort and age at maturity in different ways, depending on their effect on growth trajectories.

The first goal of this study was to test these predictions with data from 17 populations of lacustrine brook trout of the Canadian Shield, southern Quebec. This species provides a good model to study the effects of both competition and fish exploitation on the life history of a freshwater fish because unexploited and exploited populations, living with and without competitors (cyprinid and catostomid species), occur in adjacent lakes of the same area. Furthermore, the effects of competition from cyprinids and catostomids on the ecology of brook trout are well documented in this system (Magnan 1988; Tremblay and Magnan 1991; Lacasse and Magnan 1992). The second objective of the study was to explore how interspecific competition and fish exploitation affect growth and an index of survival with the aim of better understanding the mechanisms underlying the observed variations in reproductive effort and age at maturity.

Materials and methods

Study lakes

The 17 study lakes are located in two adjacent study areas in the province of Quebec (Canada): Lakes Arlequin, Bellerive, Ford, Franciscains, Grillon, Lajoie, Michelin, Petit, Sauterelle, Vautour, and Vert are situated in the Mastigouche Reserve (46°34′N, 73°34′W), and Lakes Alphonse, Archange, Baie-verte, Formont, Sud-est, and Theode are in La Mauricie National Park of Canada (46°46′N, 73°00′W). These lakes are typical oligotrophic temperate-zone lakes with respect to surface area, mean depth, conductivity, Secchi disk transparency, and thermal stratification (Magnan 1988; Environnement Canada 1990; Lacasse and Magnan 1992). Four of these brook trout lakes were unexploited and contained allopatric populations, four were unexploited with sympatric populations, three were exploited by sportfishing with allopatric populations, and six were exploited with sympatric populations (Table 1). Exploited brook trout populations had been subject to sportfishing for at least 20 years, and their exploitation is carefully controlled by governmental agencies (Mastigouche Reserve, Ministère des Ressources Naturelles et de la Faune (Faune Québec), and La Mauricie National Park of Canada, Parks Canada). Fishery managers tend to keep the maximum annual yield of these lakes in equilibrium with the mean fish weight and fishing success, which should correspond to the maximum sustainable yield (Ricker 1975). However, lakes from La Mauricie National Park of Canada tend to be underexploited for conservation purposes.

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Table 1. General characteristics of allopatric, sympatric, exploited, and unexploited brook trout (*Salvelinus fontinalis*) populations in the 17 study lakes (Canadian Shield, southern Quebec).

Lake	Surface area (ha)	Length at 2 years old (mm)[a]		GSI ($g \cdot g^{-1}$)[b]	Mean age at maturity (years)		Maximum age (years)	Fishing yield ($kg \cdot ha^{-1}$)[c]	Other fish species (BPUE)[d]		
		Females	Males		Females	Males			Se	CaCo	CaCa
Arlequin	6	189	205	0.113	2.2	2.7	3	—	—	—	—
Bellerive	10	200	210	0.076	3.1	2.7	4	—	—	—	—
Baie-verte	10	197	195	0.090	4.0	3.3	6	—	—	—	—
Theode	18	166	168	0.076	4.2	3.5	7	—	—	—	—
Franciscains	7	190	156	0.032	2.6	2.1	3	7.43	—	—	—
Petit	8	210	183	0.052	2.3	2.3	3	6.90	—	—	—
Vautour	7	160	173	0.069	2.7	2.4	3	6.55	—	—	—
Grillon	5	189	205	0.096	2.7	2.8	4	—	0.68	—	—
Sud-est	14	211	241	0.065	4.8	3.6	7	—	0.04	—	—
Michelin	8	201	203	0.116	3.3	3.2	4	—	0.69	4.84	—
Ford	32	201	216	0.058	2.8	2.7	4	—	—	3.67	0.37
Alphonse	13	196	200	0.093	4.1	4.3	6	3.69	0.02	—	—
Archange	17	163	174	0.088	4.5	4.3	6	1.87	0.10	—	—
Formont	22	223	207	0.092	4.0	4.8	5	2.46	0.10	—	—
Lajoie	10	183	173	0.045	2.7	2.3	4	3.28	—	1.50	—
Sauterelle	6	229	253	0.064	2.6	2.2	3	2.25	—	3.86	—
Vert	16	207	205	0.019	2.2	2.1	3	2.39	0.01	7.31	—

[a]Back-calculated length (see text).
[b]GSI, gonadosomatic index (ratio of gonad mass to total body mass).
[c]See Materials and methods.
[d]BPUE, biomass per unit of effort (kg fish·gill $net^{-1} \cdot day^{-1}$); Se, *Semotilus* spp. (creek chub (*Semotilus atromaculatus*); pearl dace (*Margariscus margarita*, formerly *Semotilus margarita*)); CaCo, white sucker (*Catostomus commersoni*); CaCa, longnose sucker (*Catostomus catostomus*).

In addition to brook trout, sympatric populations contained creek chub (*Semotilus atromaculatus*), pearl dace (*Margariscus margarita*, formerly *Semotilus margarita*), white sucker (*Catostomus commersoni*), longnose sucker (*Catostomus catostomus*), or a combination of these (Table 1). In this system, the intensity of interspecific competition varies from zero (allopatric brook trout populations) to intermediate (in sympatry with cyprinids) to high (in sympatry with catostomids) (see Bourke et al. 1999). So, the study lakes provided good gradients in the intensity of both fishing and interspecific competition (Table 1).

Fish sampling

Lakes in the Mastigouche Reserve were sampled from 5 to 23 September 1984 and those in La Mauricie National Park of Canada were sampled from 23 September to 13 October 1999. These differences in sampling year and site may have introduced some variation in the response variables and statistical analyses. We did not use a dummy variable coding for sampling year and study site in the statistical analyses described below because (*i*) we could not distinguish the variation related to the sampling year from that related to the study site (although the Mastigouche Reserve and La Mauricie National Park of Canada are adjacent and part of the same hydrographic system) and (*ii*) we would have had an unbalanced sample size between study sites (of our 17 study lakes, only six were in La Mauricie National Park of Canada). To examine this, we performed all statistical analyses described below with and without the second data set from La Mauricie National Park of Canada (Table 1). The results were comparable, indicating that there was no observable effect of sampling date or study site.

Fish were captured with experimental multifilament gill nets (1.8 m deep × 38 m long with stretched mesh of 25, 32, 38, 51, 64, and 76 mm). The nets were set randomly, perpendicular to the shore, with small (25 mm) and large (76 mm) meshes alternating from the shore among gill nets. We varied the number of nets used (between 4 and 12) among lakes to capture a minimum of 100 brook trout within 4–5 days (it took 1–2 days to get this sample size with four nets in allopatric populations compared with 4–5 days with 12 nets in brook trout – white sucker lakes). Fishing took place for 16–24 h and always covered the period between 1800 and 0900 local time. Fish were kept on ice until processed in the laboratory, which occurred on the same day. All fish captured were identified, weighed (±0.1 g), and measured (±1 mm total length). Each brook trout was classified as mature or immature, and mature females were weighed (±0.1 g) with and without their gonads. Scales and otoliths were sampled in 1984 and 1999, respectively, for age determination (see details on age determination below). Scales from the left side of brook trout, between the dorsal fin and lateral line, were mounted between acetate sheets (Magnan and FitzGerald 1983).

Dependent variables

We used four dependent variables to test our hypotheses: indices of survival and growth, age at maturity, and gonadosomatic index (GSI) (ratio of gonad mass to total body mass) as a surrogate of reproductive effort by females.

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Because of the sampling gear used (low catchability of ages 0+ and 1+), it was not possible to estimate the true survival rate (*S*) (Ricker 1975). We used catch per unit of effort (CPUE) (number of fish captured per gill net per day of fishing) to determine if brook trout survival is affected by fishing and interspecific competition and thus if these latter factors affect reproductive effort and age at maturity of trout through their effects on survival. When using CPUE to determine if brook trout survival is affected by fishing and interspecific competition, we assume that all lakes have roughly the same density of juveniles and subadults. If this assumption is true, we predict that the effects of exploitation and interspecific competition will be additive on CPUE of brook trout (see Results). It is important to note that such a use of CPUE as an index of survival related to fishing and interspecific competition does not give any information about the other causes of natural mortality. It has been shown that the presence of white sucker decreases the CPUE of juvenile and adult brook trout (Lachance and Magnan 1990; Venne and Magnan 1995) and that fish exploitation imposes a direct mortality on larger individuals in a population (Jennings and Kaiser 1998; Hall 1999).

We used the back-calculated length at ages 1 and 2 as indices of juvenile and adult growth, respectively. Length at age 1 was selected for juvenile growth because no individuals mature before 1 year of age in brook trout (Power 1980). Length at age 2 was used for adult growth because many populations had mature 2-year-old individuals (Table 1). A detailed description of the methods used to prepare the scales and otoliths and determine brook trout age can be found in Magnan and FitzGerald (1983). These authors showed that the two structures give comparable results when estimating the age of brook trout. The first author of the present paper (P. Magnan) was involved in age determinations of the two samples (1984 and 1999) to insure uniformity in the interpretation of these bone structures. Age was estimated by two readers. When the first two readings differed, two other readings were completed; the sample was discarded if there was still no agreement. Back-calculations were made following Magnan and FitzGerald (1983). For the 1984 samples, the growth increments were measured to the nearest 0.01 mm from marks drawn on a line from a clear chamber mounted on a dissecting microscope with a digitizing table interfaced with the DISBCAL-1989 software (Missouri Department of Conservation, Fisheries Division, Jefferson City, MO 65102-0180, USA). For the 1999 samples, growth increments were also measured to the nearest 0.01 mm but using an image analyzer (Cohu color camera, 8210 Series NTSC/Y-C; Cohu, Inc., San Diego, CA 92123-1827) mounted on a dissecting microscope connected to a computer and interfaced with the Sigma Scan Pro® program (version 4.0). We back-calculated body lengths at previous ages following the two proportional back-calculation methods: the scale-proportional hypothesis and the body-proportional hypothesis (Francis 1990). Because we got some negative back-calculated lengths when using the scale-proportional hypothesis method, we used back-calculated lengths computed with the body-proportional hypothesis method (Francis 1990).

Age at maturity of male and female brook trout were considered separately in this study, whereas reproductive effort was estimated only for females. We used the mean age of mature individuals as an index of age at maturity (i.e., age when 50% of the individuals are mature). This was necessary because the life span of many of our exploited populations was very low (3–4 years) (Table 1), and thus, it was not possible to accurately determine the cumulative frequency of mature individuals needed to estimate the size and age at maturity from probit analyses or the first occurrence at 50% maturity (Trippel and Harvey 1991). The estimation of age at maturity from probit analyses was possible in only four of our populations. Simple age structure effects will cause the mean age of mature fish to decrease as adult mortality increases. However, the short adult life span of brook trout should ensure that most of our observed variation in mean age of mature fish results from real differences in the age at maturity. This contention is confirmed by the fact that among females, the youngest age group exhibiting a level of maturity equal to or greater than 50% was highly correlated with the mean age of mature females ($r = 0.76$, $p < 0.001$, $n = 17$). Such a comparison was not possible for males because the youngest male age group exhibiting a maturity rate greater than 50% was very similar across all populations (either 2 or 3 years). So, we considered that the mean age of mature individuals was a good index for representing the among-lake variability in age at maturity for both males and females. In the computation of mean age at maturity, we set the age of mature individuals as well as their maximum age at the end of their growing season because if not captured, these fish would have completed this growth when spawning (e.g., an age-1+ individual that was mature at the moment of capture would have reproduced at 2 years old, some weeks later). Finally, the GSI should be a good approximation of reproductive allocation in brook trout because females do not provide parental care (Power 1980; Hutchings 1993).

Independent variables

We used four independent variables to predict the age at maturity and reproductive effort of brook trout from the 17 study lakes: CPUE of brook trout as an index of survival (described above), lengths at ages 1 and 2 as indices of juvenile and adult brook trout growth, respectively (described above), mean annual brook trout yield (kilograms per hectare) of the last 5 years as a measure of fish exploitation (described above), and biomass per unit of effort (BPUE) (kilograms per gill net per day) of competing species as a measure of interspecific competition. We used the BPUE instead of CPUE for competing species because the different density – body size relationships among these (small cyprinids versus large catostomids) could bias the estimation of the overall impact of competitors on the available resources and thus on brook trout (see Brodeur et al. 2001). We also used in independent models the adult to juvenile growth ratio instead of length at ages 1 and 2 as growth indices (see Statistical analyses) to test the hypothesis suggested by Hutchings (1993) that the adult to juvenile growth ratio, not growth rate per se, is the more significant parameter when predicting life history strategies. The adult to juvenile growth ratio was computed as the back-calculated length of adults from the beginning to the end of their second year of life divided by the length of juveniles at the end of their first year of life. We also used CPUE and mean annual yield of

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brook trout and BPUE of competing species as independent variables in other models to predict growth of male and female brook trout (juveniles and adults).

Statistical analyses

Even though the basic design of our study was suited to testing with a two-way analysis of variance (ANOVA) (i.e., comparison of response variables in allopatric versus sympatric and exploited versus unexploited brook trout populations), we instead used multiple linear regressions to predict the age at maturity (males and females) and reproductive effort (females) from all of the independent variables described above. This was done to determine the independent contribution of growth, survival, fishing, and interspecific competition on age at maturity and reproductive effort, considering that a part of growth and survival could be explained by fishing and interspecific competition. Furthermore, linear regression is more powerful than ANOVA to test for the main effects of fishing and interspecific competition in our study: with the ANOVA, we would have used these independent variables as categorical variables, which is less sensitive than using the raw data of mean fishing yield and BPUE of competing species (which are continuous variables). We also used multiple linear regressions to predict growth parameters of brook trout from survival, fishing, and interspecific competition to better understand factors that affect these parameters. Finally, we used simple linear regressions to test whether reproductive effort (GSI) was inversely related to age at maturity, a current prediction of life history models. All models involving growth parameters (back-calculated length at 1 and 2 years) were also run with the adult to juvenile growth ratio instead of length at 1 and 2 years (see above).

All variables that were not normally distributed were log transformed. In the stepwise procedure of the multiple linear regression, we used both the forward and backward variable selection procedures when more than two independent variables were used in the models (i.e., models predicting growth parameters, age at maturity, and GSI). In most cases, the same regression equation was obtained by both approaches, but in case of disagreement, preference was given to the best model, as indicated by the highest R^2 and the lowest mean square error associated with the estimate. Collinearity between the independent variables was evaluated by examination of the pairwise correlation coefficients. The independent variables that were highly correlated (e.g., $r = 0.7–1.0$) were not considered simultaneously in the regression analysis. After variable selection was completed, models were also screened for multicollinearity by examination of the tolerance level of individual variables (Tabachnick and Fidell 1996). The tolerances of individual variables were greater than 0.80 in all final equations. Residual scatterplots, normal probability plots, and partial residual plots were used to determine if the assumptions of the multiple linear regression were satisfied (i.e., normality, linearity, and homoscedasticity of residuals; Tabachnick and Fidell 1996). To determine if the variable selection obtained with the stepwise procedure gave the most plausible model, we compared models obtained with this procedure with the set of all possible models containing two or more independent variables. Akaike's Information Criterion (AIC) corrected for small samples (AIC_c) was used to compare and rank all of the candidate models (Burnham and Anderson 2002). This approach for model selection helps to avoid both under- and over-fitting of the data and thus provides an objective way of selecting the model that accounts for the most variation with the fewest variables. The AIC_c was used to select the best model (i.e., the one having the smallest AIC_c value) by deriving the relative plausibility of each fitted model (Burnham and Anderson 2002). All analyses were done with SYSTAT version 8.0 software (Wilkinson 1998).

Results

The comparison of all possible candidate models developed with the AIC procedure revealed that the models produced with the stepwise variable selection in the multiple regression analyses were the most plausible models. Therefore, only the results of this latter procedure will be presented here.

CPUE and BPUE of male and female brook trout

The CPUE of brook trout females was inversely related to the intensity of fishing ($p = 0.050$) and to the BPUE of competing species ($p = 0.003$) (Table 2; Fig. 1). Fishing yield and BPUE of competing species explained 15.1% and 38.8%, respectively, of the variation in CPUE of brook trout females (Table 2). The regression model explaining the CPUE of males was marginally significant ($p = 0.071$) and showed the same trend as that of females (i.e., negative effects of fishing yield and BPUE of competing species on the CPUE of brook trout) (Table 2; Fig. 1). As for CPUE, the BPUE of brook trout females was inversely related to the intensity of fishing ($p = 0.002$) and to the BPUE of competing species ($p < 0.001$) (Table 2; Fig. 1). Fishing yield and BPUE of competing species explained 24.7% and 51.2%, respectively, of the variation in BPUE of brook trout females (Table 2). The regression model explaining the BPUE of males was significant ($p = 0.004$) and explained 54.4% of the variation (Table 2; Fig. 1). This model retained only the BPUE of competing species as a significant determinant ($p = 0.002$) and the fishing yield as a suppressive variable (i.e., an independent variable that is not significantly correlated with the dependent variable but that is useful in the model because it suppresses some variance in the other independent variable; Tabachnick and Fidell 1996). This model also showed negative effects of BPUE of competing species and fishing yield (although this latter effect was not significant, $p = 0.066$) on the BPUE of brook trout males (Table 2).

Growth

None of the models predicting the growth of male and female juvenile and adult brook trout were significant (Table 2). Only the regression model predicting the growth of adult males was marginally significant ($p = 0.053$) (Table 3; Fig. 2). This model explained a total of 34.1% of the variation in growth of adult males and retained the fishing yield as a significant determinant ($p = 0.040$) and the CPUE of brook trout as a suppressive variable. This model showed negative effects of fishing yield and CPUE of brook trout (although this latter effect was not significant) on growth of adult males (Table 3; Fig. 2).

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Table 2. Best regression models predicting catch and biomass per unit of effort (CPUE and BPUE) of male and female brook trout (*Salvelinus fontinalis*).

Model		p	SE	R^2	Adjusted R^2	S_{yx}
Males						
CPUE		0.071[a]		31.4	21.6	0.87
0.11		0.595	0.21			
–0.19	Fishing yield	0.388	0.22	3.8		
–0.52	BPUE-COMP	0.028	0.21	27.6		
BPUE		0.004[a]		54.4	47.9	0.71
–0.06		0.715	0.17			
–0.35	Fishing yield	0.066	0.18	13.0		
–0.65	BPUE-COMP	0.002	0.17	41.4		
Females						
CPUE		0.004[a]		53.9	47.3	0.57
0.28		0.065	0.14			
–0.30	Fishing yield	0.050	0.14	15.1		
–0.51	BPUE-COMP	0.003	0.13	38.8		
BPUE		<0.001[a]		75.9	72.4	0.51
0.27		0.043	0.12			
–0.47	Fishing yield	0.002	0.13	24.7		
–0.72	BPUE-COMP	<0.001	0.12	51.2		

Note: The partial R^2 associated with each variable was calculated as the standardized regression coefficient times the correlation coefficient between the dependent variable and this independent variable (Tabachnick and Fidell 1996). SE, the standard error of the coefficients; S_{yx}, the standard error of the estimate; BPUE-COMP, biomass per unit of effort of cyprinids and catostomids.

[a]Probability associated with the entire model.

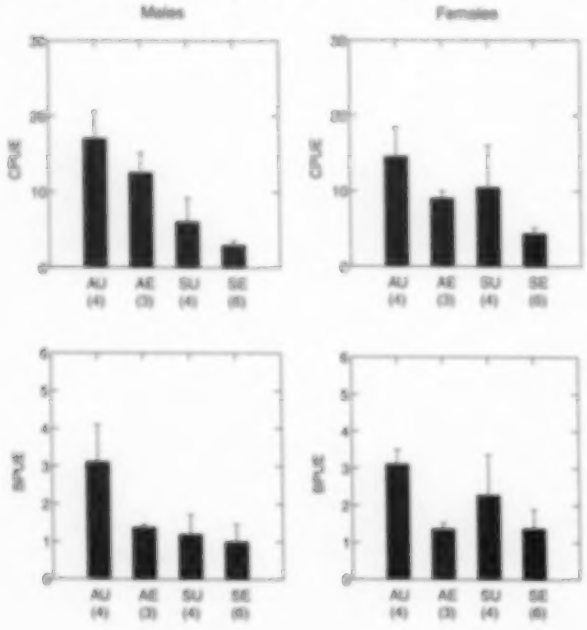

Fig. 1. Catch and biomass per unit of effort (CPUE (no.·gill net^{-1}·day^{-1}) and BPUE (kg·gill net^{-1}·day^{-1})) of brook trout (*Salvelinus fontinalis*) in allopatric (A), sympatric (S), exploited (E), and unexploited (U) brook trout populations in the 17 study lakes (Canadian Shield, southern Quebec). Data are means (bars) + standard errors (vertical lines above bars). The number of lakes in each category is given in parentheses.

Age at maturity

The multiple regression analyses revealed that ages at maturity of males ($p = 0.038$) and females ($p = 0.051$) were inversely related to mean fishing yield and competitor biomass and, to some extent, the CPUE of brook trout (significant in the regression model for males and as a suppressor variable in that of females; Table 4). These models explained 46.5% and 43.9%, respectively, of the variation in the age at maturity of male and female brook trout (Table 4). No models were significant ($p > 0.05$) or improved when using the adult to juvenile growth ratio instead of growth of juveniles and adults as independent variables.

Reproductive effort

The multiple regression analysis indicated that the GSI of females was positively related to the CPUE of brook trout ($p = 0.014$) (Table 4). This model explained 45.4% of the variation in the GSI of females and also retained juvenile growth as a suppressor variable (Table 4). Again, no models were significant or improved when using the adult to juvenile growth ratio instead of juvenile and adult growth as independent variables. Simple linear regressions also revealed that the GSI of females was positively related to their age at maturity in exploited lakes (exploited lakes: $p = 0.003$, $R^2 = 0.73$; unexploited lakes: $p > 0.05$) (Fig. 3). Although not significant, the GSI of females tended to be inversely related to their age at maturity in unexploited lakes.

Discussion

The CPUEs of male and female brook trout were significantly lower in sympatric than in allopatric populations and in exploited than in unexploited lakes, supporting that the effects of these factors were additive and thus that brook trout

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Table 3. Best regression models predicting growth of male and female juvenile (back-calculated length at 1 year) and adult (back-calculated length at 2 years) brook trout (*Salvelinus fontinalis*).

Model		*P*	SE	R^2	Adjusted R^2	S_{xy}
Males						
Juvenile growth		0.462[a]		17.4	0.1	0.80
–0.18		0.410	0.21			
–0.17	Fishing yield	0.435	0.21	9.4		
0.26	BPUE-COMP	0.381	0.29	5.2		
0.43	CPUE-SAFO	0.296	0.38	2.8		
Adult growth		0.053[a]		34.1	24.7	0.71
–0.04		0.814	0.18			
–0.40	Fishing yield	0.040	0.17	19.9		
–0.39	CPUE-SAFO	0.104	0.23	14.2		
Females						
Juvenile growth		0.281[a]		24.7	7.3	0.80
–0.28		0.410	0.21			
–0.05	Fishing yield	0.435	0.21	0.4		
0.43	BPUE-COMP	0.381	0.29	15.2		
0.71	CPUE-SAFO	0.296	0.38	9.2		
Adult growth		0.441[a]		11.0	0.1	0.67
–0.19		0.274	0.17			
–0.06	Fishing yield	0.710	0.16	1.0		
–0.27	CPUE-SAFO	0.214	0.21	10.0		

Note: The partial R^2 associated with each variable was calculated as the standardized regression coefficient times the correlation coefficient between the dependent variable and this independent variable (Tabachnick and Fidell 1996). SE, the standard error of the coefficients; S_{xy}, the standard error of the estimate; BPUE-COMP, biomass per unit of effort of cyprinids and catostomids; CPUE-SAFO, catch per unit of effort of brook trout.

[a]Probability associated with the entire model.

survival is lower in exploited and sympatric populations. The fact that we considered replicates of each treatment level prevented us from interpreting outlier or atypical populations (e.g., stunted populations). It is well documented that fishing, through the harvesting of larger individuals, decreases adult survival (Jennings and Kaiser 1998; Hall 1999). Studies done in our system also indicate that mortality associated with competition occurs in both juvenile and adult brook trout. Venne and Magnan (1995) found that young-of-the-year brook trout (captured in June) were 90% less abundant in five lakes containing white sucker than in five others containing allopatric brook trout, indicating that there is an important bottleneck on juvenile brook trout survival in the presence of white sucker. Furthermore, Lachance and Magnan (1990) observed that the recoveries (creel census) of stocked age-1+ and age-2+ brook trout (wild, domestic, and hybrid strains) were 75% lower in three lakes with white sucker than in three allopatric lakes.

One prediction of life history models is that low adult survival will favour early maturity (Roff 1984; Stearns and Koella 1986; Hutchings 1993). Based on the tenets of these models, we predicted that interspecific competition and fish exploitation would promote early maturity through their negative effects on adult survival. This prediction was supported by our data on lacustrine brook trout populations of the Canadian Shield: the ages at maturity of males and females were inversely related to the intensity of both fishing and interspecific competition by cyprinids and catostomids. In an analysis of 84 populations of 49 species, Rochet et al. (2000) found that increasing fishing pressure decreases age at maturity. However, the inverse relationship between the age at maturity and CPUE of brook trout (significant for males and as suppressive variable for females) is more difficult to interpret. In these models, CPUE of brook trout (when significant) explained a given proportion of the variation in the age at maturity, after the effects of fishing and interspecific competition were accounted for in the regression models. If CPUE of brook trout is a good index of the other causes of mortality, then this component of mortality does not support the current hypothesis that low adult survival will favour early maturity. However, one must be cautious when interpreting CPUE of brook trout as an index of survival in this context (i.e., in a model considering simultaneously the effects of fishing, interspecific competition, and other causes of mortality) because fishing and interspecific competition might drive mortality of brook trout in this system.

Life history models also predict that high juvenile growth will favour early maturity (Roff 1984; Stearns and Koella 1986; Hutchings 1993). We did not find any significant effect of fishing and interspecific competition on growth of juvenile or adult brook trout. Furthermore, the regression model predicting the age at maturity did not retain any growth parameters. It was difficult to predict the effect of fishing and interspecific competition on growth trajectories and thus on the age at maturity of brook trout. In some cases, it has been shown that growth is reduced in the presence of competing species. For example, juvenile pumpkinseed growth is reduced in the presence of bluegills (Mittelbach 1988; Osenberg et al. 1992), and Fox (1994) showed that these decreases in growth were associated with delayed maturity and lower reproductive effort in pumpkinseed. However, factors other than juvenile growth may have contributed to the observed differences in life histories between sympatric and

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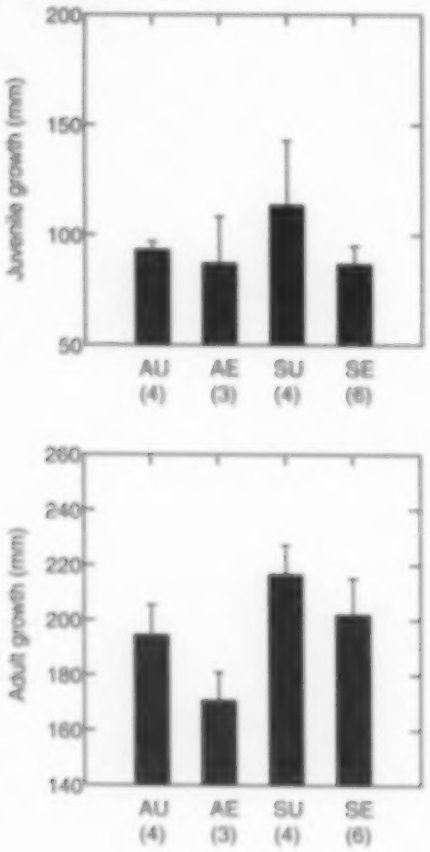
Fig. 2. Growth of juvenile (back-calculated length at 1 year) and adult (back-calculated length at 2 years) brook trout (*Salvelinus fontinalis*) males in allopatric (A), sympatric (S), exploited (E), and unexploited (U) populations in the 17 study lakes (Canadian Shield, southern Quebec). Data are means (bars) + standard errors (vertical lines above bars). The number of lakes in each category is given in parentheses.



allopatric pumpkinseed populations, like differences in adult compared with juvenile survival, environmental factors among lakes, and piscine predators (Fox 1994). Brodeur et al. (2001) found that competitive release from white sucker, through mass removal, significantly improved juvenile and adult brook trout growth in the lakes where white sucker removal was highest. We thus expected a similar growth compensation in sympatric and exploited populations owing to the effect of competitive release at the intraspecific level (as both fishing and interspecific competition decrease brook trout abundance). It is possible that when they are at equilibrium with competition and fishing exploitation, sympatric and exploited brook trout populations experience growth similar to allopatric and unexploited populations. Despite this, there is still an incongruity with respect to the current prediction of life history models: after controlling for the effects of interspecific competition and fishing, the multiple regression did not retain any growth parameters as factors explaining the age at maturity.

Finally, life history models predict that low adult survival and high juvenile growth will be associated with high reproductive effort (Roff 1984; Stearns and Koella 1986; Hutchings 1993). The analysis by Rochet et al. (2000) on 49 exploited species supported the hypothesis based on survival: decreased survival (associated with increased fishing pressure) was related to increased reproductive effort. We did not find any significant effect of interspecific competition or consistent effect of fishing on the GSI of females. Female GSI was directly related to an index of adult survival (in all populations) and with the age at maturity (in exploited populations). These results are opposite to the predictions of life history models under the assumption that survival is directly related to growth. Hutchings (1993) suggested that a positive association between growth and survival is not a prerequisite for the prediction of life history models to be true. Anadromous salmonids provide an example of how the selective benefits of high reproductive effort can overcome the selective disadvantages of high adult mortality. Compared with freshwater habitats, the marine environment provides a rich food resource for salmonids and allows for rapid growth with a concomitant high reproductive effort, despite the significantly higher mortality experienced at sea (Hutchings 1993). Such a phenomenon might also occur in freshwater ecosystems. Compared with the growth of many freshwater brook trout populations (Scott and Crossman 1973; Power 1980; Hutchings 1993), our populations are among the fast-growing ones. This high growth is probably related to habitat type (individuals from lake populations are usually larger than individuals from small streams) and latitude (low latitudes provide better conditions for growth than higher ones through the effect of latitude on the length of the growing season; Venne and Magnan 1989; Conover 1992; Duchesne and Magnan 1997). So, it is possible that, over a given juvenile growth rate, the benefits of high reproductive effort can overcome the advantage of delaying reproduction and reducing reproductive effort even when adult survival is high (i.e., observed positive relationship between GSI and the index of female survival). It is also possible that in a fast-growing population, survival, not growth, would be the main determinant of the age at maturity and that the reproductive effort would not be a main issue (because rapid growth is concomitant with high reproductive effort, and thus, reproductive effort will be high in any case). In the context of fast-growing populations, the difference in growth related to competition and fishing might not be detectable, but the rapid growth of juveniles is still related to high reproductive effort and thus conforms to the life history predictions. There might not be enough variation in growth in these populations to observe any effect of this parameter on the age at maturity and reproductive effort.

The above hypothesis about fast-growing populations could explain why the adult to juvenile growth parameter was not a better predictor than length at ages 1 and 2 in our statistical analyses because in this case, both juveniles and adults are fast growing. This hypothesis could also explain why we did not observe any compensatory growth response of brook trout in sympatric and exploited lakes due to the decrease in intraspecific competition. Juvenile and adult growth may be high enough to prevent any growth response given the level of competitive release. Finally, our results

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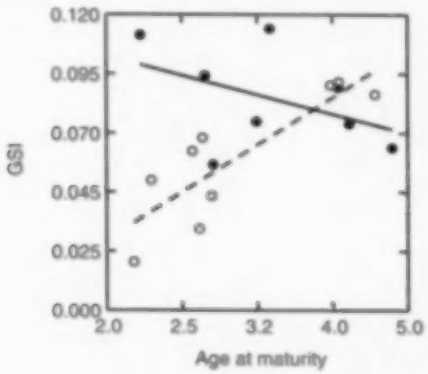
Table 4. Best regression models predicting the age at maturity of male and female brook trout (*Salvelinus fontinalis*) and the gonadosomatic index (GSI) of females.

Model		*p*	SE	R^2	Adjusted R^2	S_{xy}
Males						
Age at maturity		0.038[a]		46.5	34.2	0.83
–0.02		0.906	0.20			
–0.46	Fishing yield	0.041	0.21	19.7		
–0.58	CPUE-SAFO	0.047	0.24	13.4		
–0.70	BPUE-COMP	0.012	0.25	13.4		
Females						
Age at maturity		0.051[a]		43.9	31.0	0.84
0.36		0.143	0.23			
–0.57	Fishing yield	0.032	0.24	11.8		
–0.77	CPUE-SAFO	0.072	0.39	16.5		
–0.81	BPUE-COMP	0.014	0.29	15.6		
GSI		0.014[a]		45.4	37.6	0.67
–0.11		0.546	0.17			
0.51	CPUE-SAFO	0.034	0.22	32.0		
0.38	Juvenile growth	0.084	0.21	13.4		

Note: The partial R^2 associated with each variable was calculated as the standardized regression coefficient times the correlation coefficient between the dependent variable and this independent variable (Tabachnick and Fidell 1996). SE, the standard error of the coefficients; S_{xy}, the standard error of the estimate; BPUE-COMP, biomass per unit of effort of cyprinids and catostomids; CPUE-SAFO, catch per unit of effort of brook trout.

[a]Probability associated with the entire model.

Fig. 3. Relationship between the gonadosomatic index (GSI) ($g \cdot g^{-1}$) and the mean age at maturity (years) of females in exploited (broken line, open circles) and unexploited (solid line, solid circles) lakes of the Canadian Shield, southern Quebec. Note that the figure shows untransformed data on logarithmic scales.



suggest that survivorship is more important than growth in predicting age at maturity. Fox (1994) reached this conclusion with pumpkinseed and discussed the importance of mortality relative to growth in the evolution of life histories. There are often exceptions to the predictions of life history models (early maturity associated with slow growth and delayed maturity associated with high growth; see Hutchings 1993; Fox 1994), but these exceptions are most often explained by variations in survivorship. In contrast, predictions based on survival usually support life history models. The current life history models assume that survival is directly related to growth. However, reproductive effort and age at maturity would not be dependent on growth when survival is independent of growth, like in exploited and sympatric populations that experience low adult survival but high growth.

Whether the differences in age at maturity of the brook trout observed in our system are under genetic control or related to phenotypic plasticity of individuals cannot be determined from our experimental design. The results of Fox and Keast (1991) and Fox (1994) showed that pumpkinseed populations co-occurring with bluegills did mature significantly later and at larger sizes and tended to have lower gonadal investment than populations living in systems without bluegills. Their observations, based on winterkill events in beaver ponds and a transplant enclosure experiment, suggested a high phenotypic plasticity in the age at maturity and reproductive investment in pumpkinseed. Both brook trout fishing and the presence of cyprinids and catostomids, through bait fish introductions (Magnan 1988), are recent in our system (within the last century). The work of Brodeur et al. (2001) suggests that brook trout growth is under phenotypic control in this system: a 3-year mass removal of white sucker significantly improved juvenile and adult brook trout growth in the lakes where white sucker removal was highest. So, it is possible that early maturity in brook trout populations experiencing higher adult mortality, through interspecific competition and fishing, would be within the reaction norm of individuals.

In conclusion, our results suggest that fast-growing populations that experience high adult mortality (here through interspecific competition and fishing) exhibit life history strategies comparable with those of slower growing populations when predictions are based on survival (i.e., early maturity and high reproductive effort are associated with high adult mortality). However, the inverse relationship between growth and survival is such that growth would not be a driving factor in the evolution of life history strategies of these populations. These results thus highlight the often overriding

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importance of survival in influencing life history traits. It will be important to formalize the different growth trajectories associated with fishing and interspecific competition in future mathematical models to better understand and predict their effects on life history strategies of fishes. Such models would be useful in managing exploited species and those experiencing interspecific competition, or both.

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The effect of adaptive change in the prey on the dynamics of an exploited predator population[1]

Peter A. Abrams and Hiroyuki Matsuda

Abstract: Mathematical models examine the relationship between harvesting effort and stock size for a predator species when the prey adapts to the risk of predation. In one set of models, the prey can increase its own reproductive rate if it increases its vulnerability to the predator. In the second set of models, each of two prey species has fixed characteristics, but changes in the average characteristics within the prey trophic level occur via shifts in the relative abundance of the two species. In both models, the equilibrium predator population can increase as harvest of that species increases. In the case of two-prey models, the predator's equilibrium population always increases with an increased harvest rate if the two prey coexist and share a single resource. The predator's equilibrium population often decreases from its maximum size to zero over a very small range of harvest rates, once those rates become high enough. Because increased stock size is often used to justify increased harvest rates, this relationship poses a risk that harvest rate will increase to the point where the stock quickly collapses. The results are relevant to understanding changes in the population size of a species experiencing declining environmental conditions.

Résumé : Des modèles mathématiques examinent la relation qui existe entre l'effort de récolte et la taille du stock chez une espèce prédatrice lorsque la proie s'adapte au risque de prédation. Dans une première série de modèles, la proie peut augmenter son propre taux de reproduction si sa vulnérabilité au prédateur augmente. Dans une seconde série de modèles, chacune de deux espèces de proies possède des caractéristiques fixes, mais les changements dans les caractéristiques moyennes au niveau trophique des proies se font au moyen de modifications dans l'abondance relative des deux espèces. Dans les deux modèles, la population d'équilibre du prédateur peut croître à mesure que la récolte de l'espèce augmente. Dans le cas du modèle à deux proies, la population d'équilibre du prédateur augmente toujours en fonction de la récolte si les deux proies coexistent et partagent une même et unique ressource. La population d'équilibre du prédateur diminue souvent de sa taille maximale à zéro sur une gamme très restreinte de taux de récolte, une fois que les taux ont atteint une certaine valeur. Parce que l'augmentation des stocks sert souvent à justifier une augmentation de la récolte, cette relation entraîne le risque que le taux de récolte augmente au point que le stock s'effondre rapidement. Ces résultats sont d'intérêt pour comprendre les changements dans la taille de la population chez une espèce qui subit un déclin des conditions de son environnement.

[Traduit par la Rédaction]

Introduction

Fisheries models have largely employed a single-species perspective. Multispecies models (reviewed by Hollowed et al. 2000; Latour et al. 2003) have generally assumed that the characteristics of individual species do not change through time. Although one popular simulation package (EcoSim; Walters et al. 2000) incorporates both a multispecies approach and an assumption of transitions from vulnerable to invulnerable states, we currently lack a good understanding of the circumstances when a two-or-more-species system incorporating adaptive evolution or behaviour will exhibit dynamics that are fundamentally different from those of single-species systems. Understanding the properties of models with small numbers of species is important in determining what factors should be included in larger scale simulation models and in understanding the dynamics of those larger models.

An earlier article (Matsuda and Abrams 2004) described how population cycles and (or) adaptive change in the predator could qualitatively change the relationship between harvesting effort applied to the predator and predator population size. One of the main results of that analysis was that, unlike single-species models, stock size could increase as harvest increased in both stable and unstable predator–prey systems. The present article will extend the previous one to examine the effect of adaptation in the prey population on the harvesting effort – stock size relationship for the predator. Studies of several fish species have shown that prey often exhibit costly shifts in either foraging behaviour (Turner and

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P.A. Abrams.[2] Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada.
H. Matsuda. Faculty of Environment and Information Sciences, Yokohama National University, 79-7, Tokiwadai, Hodogaya-ku, Yokohama, Kanagawa 240-8501, Japan.

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[2]Corresponding author (e-mail: abrams@zoo.utoronto.ca).

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Mittelbach 1990; Fraser and Gilliam 1992; Eklöv and Persson 1995) or genetically determined life history traits (Reznick et al. 1990) in response to greater abundance of piscivorous predators. The foraging shifts are examples of life history plasticity, since they involve increased survival at the expense of decreased growth or reproduction. There is mounting evidence that adaptive changes, both behavioural and evolutionary, affect the dynamics of exploited fish populations (Heino and Godø 2002). Here, we take a general theoretical approach to determine the potential population dynamical consequences of prey adaptation in systems in which the predator is exploited.

We begin by noting some of the properties of single-species models in which the harvested stock has a relatively homogeneous population whose members have fixed characteristics and whose limiting dynamic in the absence of environmental variability is a stable equilibrium. Such a population exhibits a decrease in population size in response to an increased per capita harvest rate. The initial and ultimate responses to increased harvest are both negative in sign. In such systems, feedback control of harvest effort represents a safe method for maintaining a healthy stock size, provided stock size can be measured, fishing effort can be controlled, and the target stock size is not too small. These results are straightforward conclusions of the models presented in standard fisheries texts (e.g., Hilborn and Walters 1992; Quinn and Deriso 1999). The remainder of this article will show how adaptive change in the vulnerability of a prey species to a predator can alter these apparently intuitive conclusions.

Relationship between predator population size and predator mortality in a predator–prey system without prey adaptation

The analysis here assumes a simple predator–prey model in which the populations are not structured. The prey has density-dependent population growth with population size R and per capita growth rate $f(R)$. An average predator individual consumes prey at a rate given by $CRg(CR)$, where C is a per capita attack rate and $g(CR)$ is a decreasing function (the satiation function) describing the proportional reduction in the predator's consumption rate as the encounter rate with prey increases; this may occur because of handling time or other factors. We assume that the functional response $CRg(CR)$ increases with R. The consumed prey is converted into new predators according to a birth rate function, b, which is an increasing function of food intake rate (i.e., the functional response). The per capita death rate of predators is given by d. If predator population size is denoted N, these assumptions result in the following population dynamical model:

$$(1a) \quad dR/dt = R[f(R) - CNg(CR)]$$

$$(1b) \quad dN/dt = N[b(CRg(CR)) - d]$$

The equilibrium predator abundance N^* is determined by eq. 1a and is simply

$$(2) \quad N^* = f(R)/[Cg(CR)]$$

Increased mortality (d) of the predator is expected to increase the equilibrium resource population based on the equilibrium condition for eq. 1b. A greater R decreases the resource per capita growth rate and increases predator satiation, which means a smaller g. Thus, the equilibrium predator population may increase with its own mortality if g decreases more rapidly than f as the result of its mortality. This is possible when the predator has a saturating (i.e., Holling type 2 or 3) functional response. However, as is well known (Rosenzweig and MacArthur 1963), the fact that N^* increases with d implies that the vertical predator isocline intersects the prey isocline where the latter has a positive slope. This in turn means that the equilibrium is an unstable focus and that cycles will occur. Numerical results show that, although the mean predator population size differs from N^*, the mean also increases with the predator's own mortality (Abrams et al. 1997; Abrams 2002).

Thus, the conclusion from simple predator–prey models with fixed prey characteristics is that the predator population will only increase with its own mortality rate when there are cycles. This conclusion must be modified if the predator's per capita growth rate is directly and negatively affected by the predator population size, e.g., if d is replaced by $d_0 + l(N)$, where d_0 is a constant and l is an increasing function of predator population size. In this case, it is possible for the equilibrium predator population N^* to increase with the predator's death rate d_0 in a stable system, although this typically requires rather careful balancing of parameter values and only occurs over a narrow range of d_0. An increase in fishing mortality seems most likely to affect density-independent mortality, d_0, rather than changing the density-dependent death rate $l(N)$.

Effect of adaptive change of prey vulnerability on the relationship between predator population size and predator mortality

There are several ways in which adaptive change in prey characteristics can alter the manner in which the predator's population size changes with its own mortality. Prey vulnerability helps determine the attack rate C and changes in C are expected to have correlated effects on prey growth rate (Lima 1998). The per capita growth function of prey is assumed to increase with C and to decrease with R. Therefore, $f(R)$ in eqs. 1 and 2 must be replaced by $f(R,C)$. If f increases because of an increase in C following greater predator mortality, eq. 2 shows that this could cause an increase in N^* with increased d. In addition, an increase in both C and R following greater predator mortality can decrease the function g, which also increases N^* (see eq. 2). The increased predator satiation (smaller g) also makes it adaptive for the prey to reduce costly defences, again implying an increase in both C and the per capita growth f. The remainder of this section develops this qualitative argument by augmenting the population dynamics model (eqs. 1a and 1b) with an equation for adaptive change in the value of C, assuming that lower C implies lower f. We assume that this trait is subject to stabilizing selection in the absence of the predator so that $\partial^2 f/\partial C^2 < 0$.

We assume that the prey's per capita growth rate f is an increasing function of vulnerability C at values of C near the

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evolutionary equilibrium, implying a cost to defence. A model that describes adaptive change in an approximate manner for many circumstances (Abrams et al. 1993; Abrams 2001) assumes that the rate of change of a trait (e.g., C) in the population is proportional to the rate of change of a particular individual's fitness with its own trait value evaluated at the population mean. This corresponds to the general finding that behaviour changes more rapidly when the reward from a unit change is greatest. Similarly, genetically determined traits evolve most rapidly when the slope of the relationship between the trait and fitness is most steep. For prey adaptation in the context of eqs. 1*a* and 1*b*, the vulnerability trait changes according to

$$(3) \qquad dC/dt = v[\partial f/\partial C - Ng(CR)]$$

where v is an adaptive rate constant that scales the rate of change in the trait relative to the rate of change of population densities, and the expression in brackets is the derivative of an individual's fitness with respect to its trait, C. The derivative of individual fitness with respect to the trait determines the rate of change in the mean value of the trait in models of mutation-limited evolution (Dieckmann and Law 1996), quantitative genetic models (Abrams et al. 1993; Abrams and Matsuda 1997), and behavioural models (Taylor and Day 1997; Abrams 2001). In all of these models, eq. 3 is an approximation based on the assumption that the amount of variation in the trait C is sufficiently small. If the change is genetic, v is the additive genetic variance of the trait. If genetic or behavioural variation is depleted when C approaches extreme values, v will be a function of C (Abrams 2001).

The system consisting of eqs. 1*a*, 1*b*, 3 can be analyzed without adopting specific functional forms for f and g. It is possible to determine when the equilibrium will be locally stable and to determine how the equilibrium values of the variables change with the predator mortality d. The details of this analysis are provided in Appendix A. The condition required for N^* to increase with d is that the following derivative be positive:

$$(4) \qquad \frac{\partial N^*}{\partial d} = \frac{\dfrac{\partial^2 f}{\partial C^2}\dfrac{\partial f}{\partial R} - Ng'\left[C^2\dfrac{\partial^2 f}{\partial C^2} + R\left(\dfrac{\partial f}{\partial R} - C\dfrac{\partial^2 f}{\partial C\,\partial R}\right)\right]}{gb'(g + CRg')\left[C^2\dfrac{\partial^2 f}{\partial C^2} + R\left(\dfrac{\partial f}{\partial R} - C\dfrac{\partial^2 f}{\partial C\,\partial R}\right)\right]}$$

Appendix A discusses the signs of the terms in this expression. If the equilibrium of the system is locally stable, both the quantity in square brackets in the denominator and the entire denominator must be negative (see Appendix A). In addition, we assume that $\partial f/\partial f < 0$ because the prey's per capita growth rate declines with its own population size and $\partial^2 f/\partial C^2 < 0$, as mentioned above. Furthermore, $g + CRg' > 0$ because the functional response increases with CR (i.e., it increases with the availability of prey). These considerations mean that, if there is no satiation ($g' = 0$), the numerator of eq. 4 must be positive, eq. 4 must be negative, and the predator must therefore decrease in population size with increases in its own death rate. However, with satiation ($g' < 0$), the second of the two terms in the numerator of eq. 4, having the form $Ng'[...]$, is usually negative, making it possible for the predator to increase as its own mortality increases. One factor that contributes to an increase in predator density is the increase in prey growth owing to a larger vulnerability, C. Appendix A shows that $\partial C^*/\partial d$ has the sign of $-[\partial f/\partial R - C\partial^2 f/(\partial C\partial R)]$. Thus, unless there is a large negative interaction of the effects of C and R on prey growth, C^* will increase with d. The greater per-individual productivity of prey provides the basis for the predator population to increase.

Some of the necessary conditions for stability of eqs. 1*a*, 1*b*, and 3 have a simple form. Unfortunately, the full necessary and sufficient local stability conditions for the system consisting of eqs. 1*a*, 1*b*, and 3 is sufficiently complicated to be of little use in understanding stability, unless specific forms are adopted for the functions in the model. Here, we simply examine stability numerically using specific forms for the three unspecified functions in eqs. 1*a*, 1*b*, and 3. We assume

$$(5a) \qquad f(R,C) = r_m + r_1C - r_2C^2 - (R/K)$$

$$(5b) \qquad g(CR) = 1/(1 + hCR)$$

$$(5c) \qquad b(CRg(CR)) = b_0CRg(CR)$$

Here, the prey's per capita growth rate f changes in a unimodal fashion with the trait C and has a minimum value of r_m. Equation 5*b* implies that the predator has a Holling (1959) disk equation (type 2) functional response with handling time h. Equation 5*c* means that the birth rate function is linear; births are directly proportional to food intake with a proportionality constant, b_0. In the absence of the predator, the prey fitness is given by f, and there is quadratic stabilizing selection on the prey's trait C. The functions given by eqs. 5*a*–5*c* also permit an analytical solution for the equilibrium R, N, and C, although the formulas for the equilibrium values are quite lengthy. The equilibrium predator population may be plotted as a function of predator death rate for a particular set of parameters (Fig. 1); it is clear that the equilibrium predator population increases with mortality over the vast majority of the range of potential mortalities. The equilibrium C increases at an accelerating rate over the same range of mortalities in this example (the figure legend discusses the stability of these equilibrium values). This model is similar to a model whose dynamics were studied in Abrams and Matsuda (1997), and there are often alternative attractors (see legend to Fig. 1). Because the trait dynamics given by eq. 3 alone can result in biologically unrealistic (either very large or negative) values of the trait, the numerical results assume that there is selection for less extreme values if C approaches zero or a maximum value (see legend to Fig. 1).

It is important to note that the prediction of an increased predator population is based on the change in equilibrium population size. The initial response of the predator to an increase in its mortality is always a decrease in population size. This is followed by an increase in both the prey's abundance and its trait value, which eventually allow the predator to increase above its initial population size. We show an ex-

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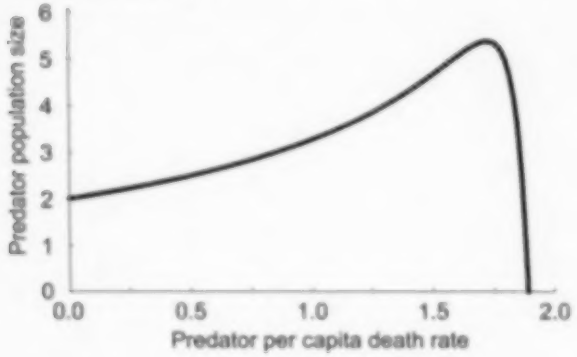
Fig. 1. Equilibrium predator population size as a function of its own per capita mortality rate for a system in which the dynamics are described by eqs. 1*a*, 1*b*, and 3 using the functional forms given by eqs. 5*a*–5*c*. The model also included minimum and maximum values of 0 and 5, respectively, for the trait C. The trait was prevented from exceeding these bounds by adding a function, $\varepsilon/C^2 - \varepsilon/(5 - C)^2$, to the right-hand side of eq. 3, with $\varepsilon = 10^{-6}$. This provides a force that pushes C away from these boundaries but has a negligible effect when C is significantly different from 0 or 5. The parameter values from eqs. 5*a*–5*c* are $r_m = 2$, $r_1 = 2$, $r_2 = 0.2$, $K = 1$, $h = 0.5$, and $b_0 = 1$. If adaptation is slow (approximately $v < 0.01$), the equilibrium is stable over most of the entire range of mortality rates shown (approximately $d > 0.15$). More rapid adaptation produces limit cycles over a broader range of low mortality rates. For example, if $v = 0.5$, the system always exhibits cycles for $d < 1.37$, and there are alternative cyclic and noncyclic attractors for approximately $1.37 < d < 1.68$.



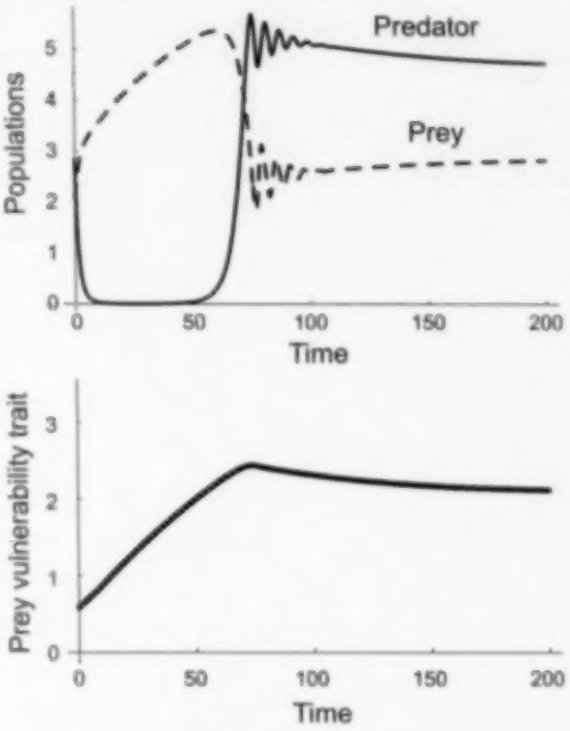
ample (Fig. 2) of the transient responses of both densities and traits to a doubling of the predator's per capita mortality rate for the system described in Fig. 1.

Effect of adaptive change in the prey community composition on the relationship between predator population size and predator mortality

A predator–prey system that contains more than a single prey species can exhibit adaptive change at the level of the prey assemblage, even when no species within that assemblage undergoes evolutionary change. Abrams and Matsuda (1997) showed that a system with two competing prey that differed in their growth rates and predator vulnerabilities could exhibit dynamics very similar to those of a single-prey model in which the single prey species had an adaptive trade-off between growth rates and predator vulnerability. This section will examine whether and when such systems can exhibit the type of increase of predator abundance with predator harvest demonstrated in the previous section.

The first model considered here consists of two prey species with a single shared resource as well as a single shared predator. This "diamond food web" has been analyzed in different ways by various authors (e.g., Armstrong 1979; Holt et al. 1994; Leibold 1996). Neither these studies nor more recent ones (Grover and Holt 1998; Abrams 1999) have

Fig. 2. Transient responses of prey, predator, and trait to a doubling of the predator mortality at time 0 for the system discussed in Fig. 1. The rate constant for change in C was $v = 0.05$. The initial system was at equilibrium for the parameter values given in Fig. 1 with a predator mortality rate of $d = 0.75$. This mortality was doubled to $d = 1.5$ at time 0.



pointed out the implications of the food web structure for the response of the predator to increased mortality. If the predator has linear functional responses to both prey, and the prey do not have any direct effects of population size on their own growth rate, then the predator's equilibrium population is independent of its own mortality. This was noted by Leibold (1996) for a similar model of the diamond web and is a consequence of the fact that the more vulnerable of the two prey types increases at the expense of the less vulnerable prey when mortality is imposed on the predator. When the predator's functional response is nonlinear, its population always increases with an increase in its own mortality as long as the two prey are able to coexist.

Although we have assumed that there is no adaptive change in either C_1 or C_2, the relative frequencies of the prey change when mortality is imposed on the predator. The resulting increase in the more vulnerable prey increases predator satiation, reducing the effective attack rates on both prey. It is these reduced attack rates that allow the predator to increase in abundance. These results can be demonstrated by an analysis of a general model with three trophic levels. Having three levels entails a shift in notation; we now denote the predator population size by P, the two prey populations by N_i, and the resource population by R. This yields a model having the following form:

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$$(6a)\quad dR/dt = R[f(R) - C_1N_1 - C_2N_2]$$

$$(6b)\quad dN_1/dt = N_1[b_1(C_1R) - d_1 - s_1PG(s_1N_1 + es_2N_2)]$$

$$(6c)\quad dN_2/dt = N_2[b_2(C_2R) - d_2 - s_2PG(s_1N_1 + es_2N_2)]$$

$$(6d)\quad dP/dt = P\{B[(s_1N_1 + es_2N_2)G(s_1N_1 + es_2N_2)] - D\}$$

The symbols that are common to this system and eqs. 1*a* and 1*b* have the same meaning. The predator's satiation function is denoted G. The parameter e measures the energetic content (or nutritional value) of prey 2 relative to prey 1, and it is assumed that energetic content (or nutritional value) of prey determines satiation. Variables N_1 and N_2 represent the populations of the two prey species. The per capita death rates of the two prey and the predator are d_i and D, respectively, while the conversion functions of resource to prey and prey to predator are b_i and B, respectively. Note that the parameters of both prey are constant; adaptive change can only occur at the prey trophic level by shifts in the abundances of the two species. The two prey species are assumed to have linear functional responses to the resource to simplify the algebra and to reduce the possibility of complex dynamics. The same techniques described in Appendix A for eqs. 1*a*, 1*b*, and 3 can be applied to this system, and the resulting expression for the change in P^* with D is

$$(7)\quad \frac{\partial P^*}{\partial D} = \frac{-PG'}{B'G[G + G'(s_1N_1 + es_2N_2)]}$$

This expression must be positive because G' is negative and B' positive by definition, and the quantity in parentheses in the denominator is the derivative of the predator's functional response with respect to food intake, which must also be positive at a stable equilibrium. It should be noted that a sufficiently large magnitude increase or decrease in D is likely to eliminate one of the prey species, and further changes in D will only have the intuitive effects on the average value of P (i.e., higher D means smaller P) if the system is stable. Note also that without predator satiation ($G = 1$, $G' = 0$), the predator's equilibrium abundance does not change with an increase in its own per capita mortality. Thus, the harvesting rate of predators would not change the equilibrium abundance as long as both prey are present.

The local stability conditions of an equilibrium of eqs. 6*a*–6*d* having all four species are quite complicated. However, the equilibrium must be stable when there is no satiation ($G = 1$), since the Jacobian matrix then satisfies qualitative stability conditions (Jeffries 1974). Simulations have shown that a wide range of parameters will produce a stable system, as long as the predator's death rate is not too low and the satiation function is not too strongly concave.

The quantitative change in predator population size with its own mortality can be illustrated for a particular version of the diamond web model. Here, we introduce some simplifications of eq. 6 that allow the equilibrium predator population size to be determined analytically. The numerical response functions b_i and B in eqs. 6*a*–6*c* are all linear, resource growth is logistic ($f(R) = r[1 - (R/K)]$), and the satiation function has the form of Holling's (1959) disk equation, $G(x) = 1/(1 + hx)$. In addition, we assume that the resource has sufficiently rapid dynamics relative to the prey that it can be assumed to always have its steady-state abundance of $(K/r)(r - C_1N_1 - C_2N_2)$. This allows the dynamics of the two prey to be reformulated as Lotka–Volterra competition equations, with the product of the two competition coefficients being unity (see Abrams 1999). We also assume that $s_2 = 0$, i.e., prey 2 is immune to predation. Thus, the model becomes

$$(8a)\quad dN_1/dt = r_1N_1[1 - (N_1 + \alpha_{12}N_2)/K_1] - s_1N_1P/(1 + hs_1N_1)$$

$$(8b)\quad dN_2/dt = r_2N_2[1 - (N_2 + \alpha_{21}N_1)/K_2]$$

$$(8c)\quad dP/dt = P[(B_0s_1N_1)/(1 + hs_1N_1) - D]$$

where B_0 is a constant, α_{ij} is the competition coefficient of prey j on prey i, and the r_i and K_i now refer to the prey rather than the resource. Equations 8*a*–8*c* have a relatively simple analytical expression for the equilibrium predator population:

$$(9a)\quad P^* = \frac{B_0r_1[B_0s_1(K_1 - \alpha_{12}K_2) - D(1 + s_1hK_1 - \alpha_{12}(\alpha_{21} + s_1hK_2))]}{K_1s_1^2(B_0 - Dh)^2}$$

$$\text{if } D < \frac{K_2s_1B_0}{\alpha_{21} + K_2s_1h}$$

$$(9b)\quad P^* = \frac{B_0r}{s_1(B_0 - Dh)}\left[1 - \frac{D}{s_1K_1(B_0 - Dh)}\right]$$

$$\text{if } D > \frac{K_2s_1B_0}{\alpha_{21} + K_2s_1h}$$

where the second solution corresponds to the case where prey 2 is excluded. Equations 9*a* and 9*b* may be plotted as a function of the predator's per capita death rate, D (Fig. 3); the different lines are characterized by different relative carrying capacities of the two prey. As can be seen from this illustration, the greatest proportional increase in predator population over the widest range of the potential mortality rates occurs when the invulnerable prey species has only a slightly smaller carrying capacity (i.e., a slight competitive disadvantage) relative to the prey species that is vulnerable to the competitor. However, the predator is relatively rare under these circumstances. The abrupt change in slope of the relationships (Fig. 3) occurs when the predator mortality is such that the less vulnerable prey is excluded by the more vulnerable prey; at still higher mortalities, the equilibrium predator population decreases.

The above results suggest that a slightly more complex food web might be capable of producing similar phenomena. In particular, it is of interest to determine how strong the competition between the two prey must be to produce the result that we have stressed above; the predator's population size increases as its own per capita mortality increases. This can be investigated by analyzing a model similar to eqs. 6*a*–6*d* but with a second resource added and some differences between the two prey in their relative utilization rates of those resources. This involves simply adding a second resource with logistic growth characterized by attack rates by the two prey species that differ in their ratio from the two attack rates on resource 1. The simplest situation involves at-

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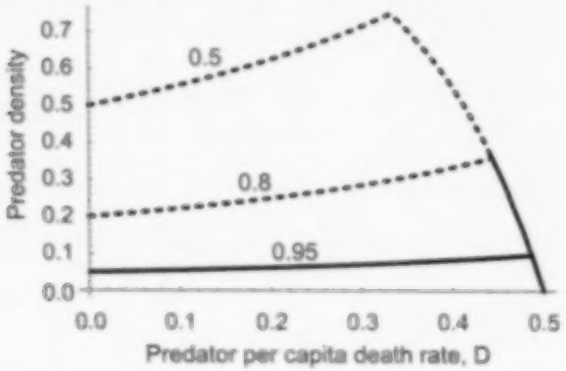
Fig. 3. Equilibrium abundance of the predator as a function of its own death rate. The underlying model is eqs. 8*a*–8*c* in which the resource dynamics are not explicit and the prey compete via Lotka–Volterra competition. The parameters are $\alpha_{12} = \alpha_{21} = 1$, $K_1 = r_1 = r_2 = 1$, $h = 1$, $s_1 = 1$, and $B_0 = 1$. Each line shows the relationship for the value of K_2 given above the line.



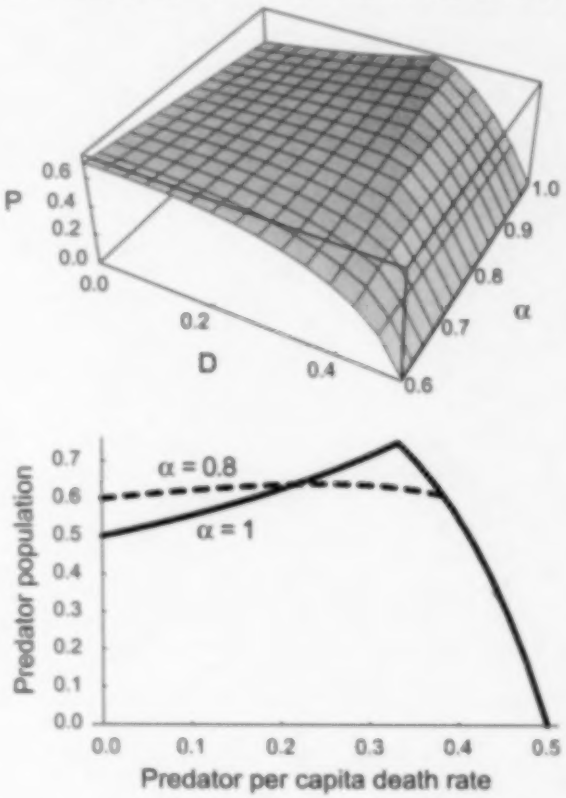
tack rates of prey 1 on the two resources (C_{11} and C_{12}) that are mirror images of those of the prey 2 (C_{21} and C_{22}), i.e., $C_{11} = C_{22}$ and $C_{12} = C_{21}$. This set of consumption rates results in competition coefficients that are equal to each other, provided both resources remain in the system. Such a system can be approximated by eqs. 8*a*–8*c*, with competition coefficients $\alpha_{12} = \alpha_{21} = \alpha < 1$. The equilibrium predator population may be plotted against its mortality rate for different values of α (Fig. 4). As α is decreased from unity, the predator mortality rate required to exclude the less vulnerable prey 2 increases. A decrease in α also decreases the range of mortality rates over which predator population size increases with increasing mortality. Thus, predator population size is often relatively insensitive to its own mortality over a wide range of mortality rates (as shown in the bottom panel of Fig. 4). When the competition coefficients are small enough ($\alpha < K_2 = 0.5$, given the other parameters in Fig. 4), the equilibrium predator population decreases monotonically with its own mortality rate. Of course, if one or both prey were capable of adaptive adjustment of a trait related to both intrinsic growth rate and predator vulnerability, the predator could decrease with harvest even when there was no competition between the prey; this case would be similar to the first model analyzed here.

Discussion

We will refer to the increase in population size that is caused by higher mortality as the hydra effect in honour of the mythological creature that grew two new heads for every one that was removed. The implications for fisheries policy of the hydra effect are quite profound. Such increases are likely to be interpreted as a license to increase harvesting rates further. However, the increase in the predator in these situations also entails a decrease in the remaining capacity of the prey to increase in population size and (or) vulnerability. There is also a decrease in the capacity of the predator to assimilate more prey because its functional response approaches its saturation level. Thus, at some point, the predator population will start to decrease rapidly in response to further increases in harvest. Of course, the equilibrium population size is not attained immediately. In addition, if mortality of the predator increases continuously over time, the population lags behind its equilibrium value, and the final decrease in the population does not have as steep a slope as these graphs of equilibrium densities might suggest. This is shown in Abrams (2002), which compares the change in actual predator population and equilibrium for several models of cycling predator–prey systems in which neither species has adaptive change. That article also shows that the population size of a predator may be a large fraction of its original equilibrium size at the point where a steadily increasing mortality passes the level where its equilibrium population size is zero. This means that there is a risk that restrictions on harvest will come too late to prevent a catastrophic decline or extinction. This same message applies to the models with adaptive change discussed here.

Even if a stock never exhibits the hydra effect (an increase in population size with harvesting), it is likely that both adaptive changes in its characteristics and its interactions with other species will affect population dynamics. Thus, both factors may often need to be studied to predict re-

Fig. 4. Equilibrium abundance of the predator as a function of its own death rate for a range of different strengths of competition. The model is given by eqs. 8*a*–8*c* and it is assumed that the two competition coefficients α_{ij} are both 0.5. The other parameter values are $K_1 = r_1 = r_2 = 1$, $h = 1$, $s_1 = 1$, and $B_0 = 1$.



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sponses to harvesting or to environmental changes. There have been other calls for more consideration of behavioural effects in understanding fisheries systems (e.g., Dill et al. 2003), but we have previously had few examples of when and why adaptive behaviour might alter the predictions of single-species approaches.

The predator's functional response has been shown to play an important role in the results obtained here. If the predator's response is linear (Holling type 1), neither of the categories of model studied here (adaptive prey or replacement of competing prey) predicts a hydra effect in the predator population. This is also true of at least some other functional responses that lack satiation. Here, we briefly describe some unpublished results on the effects of changing the two-prey model (eqs. 6*a*–6*d*) so that it has the simplest predator functional responses used in the popular computer package EcoSim (Walters et al. 1997, 2000). In this case, the functional response of a predator with population P to prey species i with population N_i is assumed to be $C_iN_i/(Q_i + w_iP)$, where C_i, Q_i, and w_i are constants. This is based on a model of random movement between vulnerable and protected states (Abrams and Walters 1996) rather than the adaptive defense assumed by eq. 3 in our analysis. Because of the lack of predator satiation in this response, the effect of mortality on the predator is similar to that in a comparable model with linear functional responses, i.e., no change in equilibrium predator density. We could also modify eqs. 6*a*–6*d* so that the two prey species, as well as the predator, have the simplest possible EcoSim functional responses. Because of the dependence of prey functional responses on their own population density, competition between the prey is reduced and the model becomes more similar to eqs. 8*a*–8*c*. As in that model, when there is no satiation, the equilibrium predator density always declines with increases in mortality. EcoSim includes options for including both variable foraging and handling time. These use an iterative numerical procedure to determine handling and foraging times (Walters and Martell 2004). While the mathematical form of the resulting functional response differs from the responses used here, it shares the property of approaching saturation at high population levels. Any such response will often lead to predator populations that increase with increasing harvest rates, given parameter values and food web configurations similar to those explored here. There is at least some evidence for strong satiation in some fish species (e.g., Eby et al. 1995), and Koen-Alonzo and Yodzis (2005) have found at least one instance of stock size increasing with harvesting in an ecosystem model with saturating functional responses.

The models analyzed here have all been quite simple, and it is important to determine to what extent our conclusions depend on that simplicity. One question is whether competitive interactions with other predators can prevent the kind of increase in abundance with increased mortality that is demonstrated here. An increase in a second predator following increased mortality of the first might prevent any increase in prey abundance or vulnerability from increasing the first predator. Our models have also assumed that the populations are unstructured; all individuals within a species are identical with respect to both their interactions with other species and their susceptibility to harvest. There are many circumstances when structured population models have qualitatively different dynamics than do unstructured population models (e.g., Iwasa et al. 1987). Finally, it is important to investigate how coupled adaptive changes in both predator and prey are likely to affect the responses of the populations of either or both species to exploitation. It will require additional work to determine whether models incorporating these additional features differ systematically in the likelihood that a harvested species will increase over a significant range of harvest rates.

Although there are many examples of fisheries that have been overexploited, we do not know of any for which there is clear evidence that increased fishing pressure caused an increase in the population size of top predator species or conversely that decreased fishing pressure resulted in a decrease in stock size. We have searched R.A. Myers' online database (http://ram.biology.dal.ca/~myers/data.html), which provides estimates of both stock size and fishing mortality for a number of species. There are some examples where decreases in stock size occurred simultaneously with a decrease in fishing mortality (e.g., monkfish (*Lophius piscatorius*) data from the International Council for the Exploration of the Sea (1993)). However, this pattern is also consistent with a negative effect of harvesting on stock size, provided the decrease in fishing mortality is not sufficiently large. For most top predators in R.A. Myers' database, stock estimates are unavailable until after fishing pressure had been intense for some time. Thus, in most of the data sets having estimates of fishing mortality, the mortality was already relatively high when it was first measured (or at least reported). As far as we have been able to determine, past records of harvest and stock size do not provide clear evidence for the phenomena that we have predicted here.

It is possible that increases in stock size due to harvesting have never occurred because of some complexities of natural communities that are missing from the models considered here. It is also possible that such increases occurred but were not observed because reliable information on stock size is often not available during the early stages of a fishery on a given species. Because of environmental variability and variation in fishing rates, it may be difficult to assign a cause to an observed increase in abundance. It is also possible that the high initial rate and rapid increase in harvest rates for many fish stocks have meant that the fishery collapsed before any of the compensatory processes discussed here had time to operate. Restrepo et al. (1998) argued that the natural mortality rate may be used as a reasonable proxy for the maximum sustainable yield fishing mortality rate. Harvest rates in modern fisheries are usually much larger than the natural mortality rate, and they have increased rapidly when stock sizes have remained reasonably high (Pauly et al. 2002). In addition, modern fisheries have often involved harvesting of several trophic levels or sequential harvest of different predatory species (Jackson et al. 2001). Any of these conditions may have prevented an increase in predator stock sizes in response to changes in the population densities and (or) defensive traits of their prey.

Recent documentation of extensive declines in predatory fish species has brought about calls for greater consideration of the maintenance of biological diversity in fisheries regulation (e.g., Pauly et al. 2002). Such a shift would likely require that future fisheries not increase harvest rates as

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rapidly as has been typical in the past. This would make it possible to determine whether the hydra effects described here and in Matsuda and Abrams (2004) are likely to occur in natural fish communities.

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Appendix A. Stability and responses of equilibrium values to predator mortality in eqs. 1*a*, 1*b*, and 3.

To determine the change in the equilibrium R, N, and C with an increase in d, we set the left-hand sides of eqs. 1*a*, 1*b*, and 3 equal to zero and differentiate the resulting equations with respect to d, noting that the equilibrium values of the variables are implicit functions of d. This yields three simultaneous linear equations for the three quantities $\partial N^*/\partial d$, $\partial C^*/\partial d$, and $\partial R^*/\partial d$. As an example, differentiating eq. 1*a* at equilibrium yields the following equation:

$$0 = f'\frac{\partial R^*}{\partial d} - CNg'\left(R\frac{\partial C^*}{\partial d} + C\frac{\partial R^*}{\partial d}\right) - Cg\frac{\partial N^*}{\partial d} - Ng\frac{\partial C^*}{\partial d}$$

Solving this, together with the corresponding equations derived from the equilibrium conditions for eqs. 1*b* and 3, yields expressions showing how the equilibrium values of the three variables change with the predator's death rate d:

$$\text{(A1)}\quad \frac{\partial N^*}{\partial d} = \frac{\dfrac{\partial^2 f}{\partial C^2}\dfrac{\partial f}{\partial R} - Ng'\left[C^2\dfrac{\partial^2 f}{\partial C^2} + R\left(\dfrac{\partial f}{\partial R} - C\dfrac{\partial^2 f}{\partial C \partial R}\right)\right]}{gb'(g + CRg')\left[C^2\dfrac{\partial^2 f}{\partial C^2} + R\left(\dfrac{\partial f}{\partial R} - C\dfrac{\partial^2 f}{\partial C \partial R}\right)\right]}$$

$$\text{(A2)}\quad \frac{\partial C^*}{\partial d} = \frac{\dfrac{\partial f}{\partial R} - C\dfrac{\partial^2 f}{\partial C \partial R}}{b'(g + CRg')\left[C^2\dfrac{\partial^2 f}{\partial C^2} + R\left(\dfrac{\partial f}{\partial R} - C\dfrac{\partial^2 f}{\partial C \partial R}\right)\right]}$$

$$\text{(A3)}\quad \frac{\partial R^*}{\partial d} = \frac{C\dfrac{\partial^2 f}{\partial C \partial R}}{b'(g + CRg')\left[C^2\dfrac{\partial^2 f}{\partial C^2} + R\left(\dfrac{\partial f}{\partial R} - C\dfrac{\partial^2 f}{\partial C \partial R}\right)\right]}$$

The conditions for the local stability of the equilibrium point(s) are found from the Jacobian matrix of the dynamic system eqs. 1*a*, 1*b*, and 3 evaluated at the equilibrium point. Unfortunately, the full conditions for stability (conditions that the eigenvalues of this matrix have negative real parts) are very complex. However, one of the necessary conditions is that the quantity in square brackets in the denominators of the above three expressions must be negative. (This quantity is equal to a positive constant multiplied by the determinant of the Jacobian matrix.)

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A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower[1]

Michael D. Rennie, Nicholas C. Collins, Brian J. Shuter, James W. Rajotte, and Patrice Couture

Abstract: Activity costs can account for a major proportion of fish energy budgets and may trade off against observed growth rates in wild fish populations. Recent approaches to estimating activity costs in situ have used a contaminant–bioenergetic mass balance modelling approach, allowing for a broader examination of activity costs among populations compared with time-consuming alternative approaches. We report the results of this contaminant–bioenergetic modelling approach to estimating in situ activity costs compared with two alternative independent methods of assessing in situ activity costs. Comparisons were made between a fast- and slow-growing yellow perch (*Perca flavescens*) population. Contaminant–bioenergetic estimates of activity costs in the fast-growing population were 39% lower than those in the slow-growing population. Activity estimated from recorded swimming behaviours was 37% lower in the fast-growing population and 22%–29% lower in the fast-growing population based on published relationships between activity costs and axial white muscle glycolytic enzyme capacities. Consumption rates were actually 32% lower in the fast-growing population, implying that lower activity costs more than compensated for lower food intake. The agreement among the three independent measures of activity costs strongly support the idea that activity costs, rather than food intake, are a major determinant of growth differences in these two wild fish populations.

Résumé : Les coûts des activités peuvent représenter une fraction importante des bilans énergétiques des poissons, ce qui peut se faire au détriment des taux de croissance dans les populations sauvages de poissons. Les méthodes récentes d'estimation des coûts des activités in situ utilisent une modélisation énergétique de bilan de masse avec un contaminant, ce qui permet un examen plus étendu des coûts des activités chez les populations que les méthodes de rechange qui requièrent plus de temps. Nous comparons les résultats d'une telle méthode bioénergétique avec contaminant pour mesurer les coûts des activités in situ à ceux de deux méthodes de rechange indépendantes d'estimation des coûts des activités in situ. Nous avons comparé des populations de perchaudes (*Perca flavescens*) à croissance rapide et à croissance lente. Par la méthode bioénergétique avec contaminant, les estimations des coûts des activités sont 39 % plus basses dans la population à croissance rapide que dans celle à croissance basse. L'activité estimée d'après l'enregistrement des comportements de nage est de 37 % plus basse dans la population à croissance rapide; elle est de 22–29 % plus basse dans la population à croissance rapide lorsqu'elle est calculée à partir des relations publiées entre les coûts des activités et les capacités des enzymes glycolytiques des muscles blancs axiaux. Les taux de consommation sont en fait 32 % plus bas dans la population à croissance rapide, ce qui implique que les coûts réduits des activités compensent amplement l'ingestion plus faible de nourriture. La concordance entre les trois mesures indépendantes des coûts des activités vient appuyer fortement l'hypothèse selon laquelle ce sont les coûts des activités, plutôt que l'ingestion de nourriture, qui sont les facteurs explicatifs principaux des différences de croissance entre ces deux populations sauvages de poissons.

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M.D. Rennie[2] and N.C. Collins. University of Toronto at Mississauga, 3359 Mississauga Road North, Mississauga, ON L5L 1C6, Canada.
B.J. Shuter. University of Toronto, Department of Zoology, 25 Harbord Street, Toronto, ON M5S 3G5, Canada.
J.W. Rajotte. Toxicology Section, Centre of Forensic Sciences Northern Regional Laboratory, 70 Foster Drive, Sault Ste. Marie, ON P6A 3V1, Canada.
P. Couture. Institut National de la Recerche Scientifique, Centre Eau, Terre et Environment, 490 de la Couronne, QC G1K 9A9, Canada.

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[2]Corresponding author (e-mail: mrennie@utm.utoronto.ca).

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Introduction

Growth rate is a tremendously plastic characteristic of fish and can vary widely both within and among populations (Boisclair and Leggett 1989*a*). Over large north–south environmental gradients, cumulative growing degree-days often correlate with variation in growth (Power and van den Heuvel 1999). As well, annual or seasonal variations in climate and (or) water temperature may also correlate significantly with variation in growth (e.g., Claramunt and Wahl 2000; Fechhelm et al. 1992; King et al. 1999). However, these relationships can rarely account for more than 50% of the variation in growth rates observed (but see Fechhelm et al. 1992). Furthermore, if one narrows the geographic scale of comparison amongst populations of a particular fish species, effectively eliminating climatic variation between environments, wide variation in growth may still be observed among populations (Boisclair and Leggett 1989*a*). Additionally, growth in fish is optimized for a given set of environmental and ecological conditions and can trade off against increased energy allocation in behaviours such as predator avoidance (Billerbeck et al. 2001; Lankford et al. 2001). As such, it is likely that at least some component of this observed plasticity in growth is due to differences in energy allocation to active metabolism between populations. However, active metabolism remains a difficult metric to quantify in the field; a variety of methods have been employed to measure it, but almost all have come under criticism, and few of these methods have been compared with one another to judge their consistency.

Activity costs have long been hypothesized to contribute significantly to fish energy budgets (Weatherly 1966). Individual growth rate can be seen as the by-product of an optimization process that trades off the levels of energy acquisition and predation risk — associated with activities such as foraging and predator avoidance — to maximize the production of offspring (Ware 1980). Thus, the cost of activity is a primary component in the system of trade-offs that determines the life history of an animal. Understanding the role of activity in this system is an important step in identifying the factors that determine the life histories of fish.

Early models of fish bioenergetics represented activity as a small component of energy budgets (Kitchell et al. 1977). However, a number of studies in the past 15 years have shown that activity costs can be a major determinant of growth, reproduction, and survival (Boisclair and Leggett 1989*b*; Trudel et al. 2001; Pazzia et al. 2002). In particular, studies describing large-scale differences in activity (i.e., between populations over long time series, such as in Pazzia et al. 2002) and queries as to the ultimate reasons for these differences (food intake versus activity, as in Trudel et al. 2001) are beginning to surface. Answering these questions adequately requires reliable methods for quantifying activity differences in wild populations over long time scales.

Among the variety of approaches used to address the role of activity costs on the growth of organisms, some have examined trade-offs between an organism's physiological capacity for activity (Arendt 2003) and its scope for growth. Capacity for activity can be measured in the laboratory using forced swimming experiments. However, an organism's physiological scope for activity may not necessarily reflect actual activity levels observed in the field, particularly if highly variable ecological characteristics, such as food distribution and availability or the presence of predators, affect the activity of an organism. Direct behavioural observations can be used to estimate activity costs (Boisclair and Sirois 1993; Aubin-Horth et al. 1999), but this approach is extremely time consuming and expensive and difficult to apply to large-bodied or cold-water species of fish that occur outside of the littoral zone. Additionally, without a large sampling effort, observation-based methods cannot offer long-term average estimates of activity costs for populations of fish.

Another method that has been used to estimate activity in the field is the examination of lactate dehydrogenase (LDH) activities in the axial musculature of fish. Higher LDH activity indicates enhancement of anaerobic capacity and may therefore reflect recent activity levels in fish (Sherwood et al. 2002*a*, 2002*b*). Increased levels of this enzyme support activities such as burst swimming, which can account for a large proportion of activity-based metabolic costs associated with the pursuit of prey or escape from predators.

Long-term activity costs in wild fish populations may also be estimated as a function of the difference between consumption and growth estimates using bioenergetics models (Boisclair and Leggett 1989*b*; Aubin-Horth et al. 1999; Trudel et al. 2001). This approach is convenient because of the ease with which it can be applied to both current and archived data compared with other methods of estimating activity costs currently in use (Trudel et al. 2001). However, this approach has also come under criticism for a number of reasons. First, predictions made by bioenergetics models depend on the accuracy of submodels used to describe metabolic rates of fish in the field (Krohn and Boisclair 1994; Aubin-Horth et al. 1999). As a result, the error surrounding predictions derived from bioenergetics models can be greatly magnified and difficult to accurately estimate. Second, field estimates of consumption based on stomach contents can also be difficult and time consuming to estimate and are based on submodels that are subject to their own assumptions and criticisms (Grant and Kott 1999; Whitledge and Hayward 2000; Bochdansky and Deibel 2001). Third, consumption estimates that are based on contaminant accumulation models do not model contaminant elimination as a function of active metabolism, which is an assumption that has been criticized as unrealistic and one that may result in overestimates of activity rates (He and Stewart 1997). Additionally, because activity rates calculated from bioenergetic models are in part dependent on growth, activity rates estimated using this approach are not entirely independent of the growth of the fish being modelled, making it difficult to examine statistical relationships between these terms (Boisclair and Leggett 1989*b*). The sum of these criticisms has cast some doubt on estimates of active metabolism acquired using bioenergetics models. Therefore, a comparison between activity levels using this method against others would be helpful in determining the degree of consistency and (or) reliability amongst methods.

This study had two primary objectives. The first objective was to assess the validity of field-based activity costs esti-

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mated using contaminant accumulation–bioenergetics models against two other methods of estimating activity in situ (field-based observations of individual fish and LDH activity) between two populations of fish with very different growth rates and trajectories. The second objective was to add to the small set of measurements of the importance of activity relative to consumption in determining observed differences in fish growth.

Methods

Description of contaminant–bioenergetics model

The model we used is a slightly modified version from that reported by Trudel and Rasmussen (2001). The model combines the mass balance formulations for contaminants and fish mass on a daily basis using the mercury (Hg) mass balance model (MMBM, Trudel and Rasmussen 2001), with the mass balance of fish energy budgets using a traditional bioenergetics model (BM; Kitchell et al. 1977; Hewett and Johnson 1992). The MMBM models the balance of methylmercury (MeHg) in the tissues of fish, as this is the form of Hg that is most readily bioaccumulated (Mason et al. 1995; Lawson and Mason 1998; Lawrence et al. 1999). If fish total mercury (THg) and MeHg concentrations are equivalent, as they were for the fish captured in this study (Rennie 2003), then one can use fish THg as an estimate of MeHg.

The uptake of MeHg in fish is mediated via uptake through the gills (Norstrom et al. 1976; Post et al. 1996) and through absorption in the gut from diet (Leaner and Mason 2002). A number of studies have shown convincingly that in uncontaminated waterbodies (i.e., those that do not receive point-source inputs of Hg), the primary mode of uptake of MeHg in adult fish is through food, and less than 0.1% of assimilated MeHg is taken up through the gills (Lock 1975; Hall et al. 1997; Lawson and Mason 1998). Therefore, uptake through the gills in adult fish from uncontaminated waterbodies can be considered negligible. The concentration of Hg in muscle and the whole body can be assumed to be equivalent (Becker and Bigham 1995; Trudel et al. 2000; Trudel and Rasmussen 2001). One can therefore model the accumulation of MeHg in fish as

$$(1)\qquad \frac{\mathrm{dHg}}{dt} = (\alpha C_d C_i) - (E + G + K)\mathrm{Hg}$$

where Hg is the MeHg concentration of the fish (μg Hg·g^{-1} wet weight); α is the assimilation efficiency of MeHg from food; C_d is the concentration of MeHg in food (μg Hg·g^{-1} wet weight); C_i is the mass-specific food consumption rate (day^{-1}) at time t; E is a function describing the instantaneous elimination rate of Hg (day^{-1}); G is the mass-specific growth rate (day^{-1}), and K is a function describing the instantaneous loss rate of MeHg to gonads (day^{-1}). If modelled over small (i.e., 1 day) time steps, daily differences in parameter values such as E and K will be small and can be considered constants over short time increments. This allows for the integration of eq. 1 to yield

$$(2)\qquad \mathrm{Hg}_t = \mathrm{Hg}_0\, e^{-(E+G+K)t} + \frac{\alpha C_i C_d}{(E+G+K)}[1 - e^{-(E+G+K)t}]$$

where Hg_0 and Hg_t are the MeHg concentration in fish at time 0 and time t, respectively. Rearranging to solve for consumption rate yields the following equation:

$$(3)\qquad C_i = \frac{\mathrm{Hg}_t - \mathrm{Hg}_0\, e^{-(E+G+K)t}}{\alpha C_d[1 - e^{-(E+G+K)t}]}(E+G+K)$$

The MMBM (eq. 3) is solved over a daily time step and combined with the BM through the common term, C_i (C_i can be converted from units of day^{-1} to J·day^{-1} by multiplying C_i by the product of the energy density of the prey and fish weight). The BM can be expressed on a daily time step as

$$(4)\qquad W_t = W_0 + [(C_i \cdot \mathrm{ED}_{\mathrm{prey}}) - (F + U + N + R_{\mathrm{T}})]/\mathrm{ED}_{\mathrm{fish}}$$

where W_t is the fish weight (g) at time t; W_0 is the initial fish weight (g), C_i is ingestion rate (J·day^{-1}) at time t, $\mathrm{ED}_{\mathrm{prey}}$ is the energy density of prey (J·g^{-1}), $\mathrm{ED}_{\mathrm{fish}}$ is the energy density of fish (J·g^{-1}), F is losses due to egestion (J·day^{-1}); U is losses due to excretion (J·day^{-1}); N is losses due to reproduction (J·day^{-1}), and R_{T} is losses due to metabolism (J·day^{-1}). Egestion and excretion losses are functions of temperature, body size, and consumption (eq. 2 in Hewett and Johnson 1992), and all parameters for the BM are from Kitchell et al. (1977), reported in Hewett and Johnson (1992).

Consumption rate in the BM is expressed as

$$(5)\qquad C_i = C_{\max} \cdot p \cdot f(T)$$

where C_i is ingestion (J·day^{-1}) at time t, $C_{\max}$ is the maximum consumption of a fish (J·day^{-1}), described by an allometric function based on laboratory experiments, $f(T)$ is a temperature function that defines the reduction in consumption above and below the optimal feeding temperature, and p is the proportion of maximum consumption realized by a fish, a value that reflects other constraints on feeding rate.

Losses from metabolism, R_{T} from eq. 4, can be further subdivided into three components:

$$(6)\qquad R_{\mathrm{T}} = \mathrm{ACT} \cdot R_s + R_d$$

where R_d is specific dynamic action (J·day^{-1}), or heat increment, R_s represents losses due to standard metabolism (J·day^{-1}), and ACT represents energy lost to active metabolism as a multiple of standard metabolism (unitless), where $1 < \mathrm{ACT} < \infty$. Alternatively, ACT may also be further decomposed as $1+(R_a/R_s)$, where activity costs (R_a) are expressed in energetic units (J·day^{-1}).

Equations 3 and 4 are both mass balance equations. As such, C_i in eq. 3 is constrained by the balance of MeHg over the time period being modelled. This was set to equal C_i from eq. 4, which is constrained by balancing mass over the time period being modelled. By iterating both equations on a daily basis, the unique solution of p and ACT that achieve the observed final weight and MeHg concentration for the particular cohort of fish being modelled was obtained through an optimization routine. The optimization minimized the error between observed W_t and Hg_t, and modelled W_t and Hg_t, such that the average difference between observed and modelled W_t and Hg_t was less than 0.01%.

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Table 1. Input parameters of the Hg mass balance model and bioenergetics model.

Symbol	Parameter description	Value	Source
α	Assimilation efficiency	0.8	1
φ	Coefficient of Hg elimination	0.0029	2
β	Allometric exponent of Hg elimination	-0.20	2
γ	Temperature coefficient of Hg elimination	0.066	2
GSI_m	Gonadosomatic index, males	0.05	3, 4, 5, 6, 11
GSI_f	Gonadosomatic index, females	0.17	3, 6, 7, 8, 9
ED_{FX}	Ratio of energy density of ovaries to energy density of the whole fish	1.2	7, 10
ED_{FY}	Ratio of energy density of testes to energy density of the whole fish	0.85	11
ED_{prey}	Energy density of fish stomach contents	3517 $J \cdot g^{-1}$	11

Note: Source references are as follows: 1, Norstrom et al. (1976); 2, Trudel and Rasmussen (1997); 3, Norton (1997); 4, Sulistyo et al. (2000); 5, Vuorinen et al.(1992); 6, B.A. Henderson, University of Toronto at Mississauga, 3349 Mississauga Road N., Mississauga, ON L5L 1C6, unpublished data; 7, Henderson et al. (2000); 8, Nelson and Magnuson (1992); 9, Heibo and Vøllestad (2002); 10, Diana (1983); 11, Rennie (2003).

Parameterization of the model

Daily elimination of MeHg (E in eq. 3) was modelled as a function of fish size (W) and temperature (T), as described in Trudel and Rasmussen (1997):

$$(7) \qquad E = \varphi W^{\beta} e^{\gamma T}$$

where φ, β, and γ are empirically derived constants (Table 1). Assimilation of MeHg from the diet (α in eq. 3) is assumed to be 80% (Table 1). Daily losses due to spawning (K in eq. 3) are

$$(8) \qquad K = \frac{Q \cdot GSI}{365}$$

where Q is the ratio of MeHg in the gonads (C_g, μg Hg·g^{-1} wet weight) to Hg in perch (C_f, μg Hg·g^{-1} wet weight), GSI is the gonadosomatic index at spawning (Table 1), and 365 is the number of days in a year. In contrast with previous models, we estimated Q on a daily basis, following relationships determined between yellow perch (*Perca flavescens*) Hg in flesh and in the gonads. Separate equations were used for both female (Hammerschmidt et al. 1999) and male yellow perch (Rennie 2003):

$$(9) \qquad \text{Females: } (C_g = 7.656 \times 1.002^{C_f}) 0.15$$

$$(10) \qquad \text{Males: } (C_g = 21.498 \times 1.001^{C_f}) 0.168$$

Values 0.15 and 0.168 above convert concentrations from Hg per unit dry weight into Hg per unit wet weight. Losses in weight due to reproduction are modelled as a one-time loss on an arbitrary day (30 April in this model) as

$$(11) \qquad W_t = W_{t-1} - W_{t-1}(GSI \cdot ED_{F(X,Y)})$$

where W_t is the weight of the fish after spawning, W_{t-1} is the weight of fish the day before spawning, and $ED_{F(X,Y)}$ is the ratio of the energy density of the gonads to energy density of the whole fish (Table 1). Because we are interested in the mass balance to yield endpoints of this modelling exercise, differences in the modelled losses for gonads between energetic (BM) and contaminant (MMBM) processes — necessary to remain compatible with the structure of each model — will have little impact on the predictions of average accumulation and loss rates over the modelled time period, which are the primary, useful outputs of both models.

Seasonal bioenergetic estimates of C and R_a were obtained using fish Hg_0 and W_0 for a particular cohort in June and using Hg_t and W_t for the same cohort collected in August of the same year. C_d was calculated as the cohort-specific average over the two time periods. Lake temperature data was obtained from temperature loggers deployed over the growing season. Energy densities of fish were estimated from the literature at 4184 J·g^{-1} (Hewett and Johnson 1992). Caloric density of prey (stomach contents) and testes were measured directly by bomb calorimetry. Energy densities of ovaries were estimated from Henderson et al. (2000).

Error estimation

To reflect sampling error from model inputs in our bioenergetics estimates, we used Monte Carlo simulations to estimate standard errors (Trudel et al. 2000). For a particular cohort, 1000 pseudo-values of initial and final weight or Hg concentration were calculated from the sample means and standard errors, assuming a normal distribution around the mean. A suite of bioenergetic estimates was calculated for each pseudo-value. Reported bioenergetics estimates are averages of these pseudo-values; standard errors are reported for comparison (Appendix A). Many studies that model contaminant accumulation and bioenergetics choose not to estimate error around their bioenergetics estimates at all (Essington and Houser 2003; Henderson et al. 2003). Though our method of error estimation represents an overall underestimate of error propagated through the model, it is consistent with methodologies employed in contaminant models reported elsewhere (Tucker and Rasmussen 1999; Trudel et al. 2000; Trudel and Rasmussen 2001).

Species and lakes studied

Yellow perch were sampled from Plastic Lake and Shoe Lake in the Dorset region of Ontario, Canada. Shoe Lake is about 7.5 km northwest of Plastic Lake and is similar in size, bathymetry, and climate (Table 2). Shoe Lake has a slightly higher pH and is also home to piscivorous fish species, such as smallmouth bass (*Micropterus dolomieu*) and lake trout (*Salvelinus namaycush*). Importantly, yellow perch from Shoe Lake have been shown to grow faster than fish

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Table 2. Comparison of the two lakes under study.

Attribute	Plastic Lake	Shoe Lake
Latitude (°N)	45°10′830″	45°12′450″
Longitude (°W)	78°49′200″	78°54′600″
pH	5.6	6.6
DOC ($mg \cdot L^{-1}$)[a]	2.05	3.24
Mean depth (m)	8.1	5.5
Surface area (km^2)	32.6	38.6
Fish community[b]	Yellow perch, rainbow smelt, white sucker, northern redbelly dace, golden shiner, creek chub, pearl dace, brown bullhead, rock bass, pumpkinseed	Yellow perch, lake trout, smallmouth bass, rock bass, pumpkinseed, golden shiner
Average invertebrate density ($g \cdot m^{-2}$)	19.3±8.9	37.9±7.1

[a]Dissolved organic carbon.
[b]Based on data provided by the Ontario Ministry of Natural Resources (D. Flowers, Minden Office, Hwy 35 By-Pass, Minden, Ontario, Canada, personal communication) and on species encountered during the course of the study.

from Plastic Lake (Rennie 2003). Fish were collected a total of five times from both lakes over 2 years: in late June and late August in 2001 and in early May, late June, and late August in 2002. A combination of gill nets set for short periods (3 h or less), minnow traps, 4-foot trap nets (1 foot = 0.3048 m), Kushneriuk traps (Kushneriuk and Paloheimo 1984), and a 40-foot beach seine were all used to catch a wide size range of perch while minimizing mortality to incidentally captured fish. Lake temperatures were monitored throughout the growing season using temperature loggers deployed in littoral and epilimnetic habitats occupied by yellow perch.

Sampling

Fish

Captured fish were euthanized, placed in new, Hg-free Ziploc™ plastic freezer bags (Rennie 2003), and stored on ice in coolers. Fish were returned to the lab and either immediately processed or frozen at –20 °C for later processing. Fork length, total length, weight, and sex were determined for each fish collected. Otoliths and scales were collected for ageing, of which the former were used as the primary ageing structure.

White muscle for Hg analysis was dissected from the predorsal area on the left-hand side of the fish just above the lateral line, using a stainless steel scalpel blade. Fish were sampled from smallest to largest within a given catch to minimize the possibility of cross-contamination, since Hg concentration in fish tissue is correlated with body size (Somers and Jackson 1993; Gorski et al. 1999; Rennie 2003). Scalpel blades were cleaned between samples using a combination rinse of 20% HCl, clean deionized water, and wiped dry with an ultra-low Hg Kimwipe™. Tissue samples were stored in preweighed, Hg-free (Rennie 2003), 1.7-mL polyethylene microcentrifuge tubes (VWR International, Mississauga, Ontario) and frozen at –20 °C. Stomach fullness was subjectively rated on a scale of 0 to 4 (0 being empty, 4 being full). Stomachs were cut from the carcass, and contents were removed and placed individually into acid-washed glass scintillation vials that were sealed and frozen at –20 °C. The proportion of empty stomachs in each sampling period was used to help determine the feeding status of perch in our two lakes.

Invertebrates

Benthic invertebrates were the primary constituents of perch diets in our lakes (Rennie 2003). To help determine how prey density — and thus availability to perch — might affect differences in activity costs and consumption between lakes, we compared the total weight of invertebrates collected in each lake during three separate collection periods. Eight benthic invertebrate samples were collected from each lake at each sampling period, using equal sampling effort. Samples were taken with D-shaped kicknets, representing an approximate sampling area of 0.5 m^2.

Laboratory analysis

THg determination of fish muscle

Approximately 250–500 mg of wet muscle was weighed, dried overnight at 60 °C, and reweighed. A known amount of dry tissue was then transferred to clean, acid-washed test tubes, digested in 2 mL of 4:1 H_2SO_4:HNO_3 at 250 °C for 4–6 h, and allowed to cool overnight. Clean, acid-washed glass marbles were placed over the openings of digestion tubes to limit atmospheric contamination and sample loss during digestion. Digests were diluted with 10 mL of Hg-free deionized water and allowed to cool for approximately 2 hours. Two hundred µL of concentrated BrCl (Bloom and Crecelius 1983) was added to preserve samples, which were sealed with parafilm and refrigerated. Samples were analyzed within 5 days of preservation, but were typically analyzed the day following preservation. Immediately before analysis, samples were treated with 20 µL of 30% NH_2OH·HCl to reduce halogens and nitrogen oxides present in the sample, which can interfere with detection. THg was determined using cold vapour atomic fluorescence spectrometry (Tekran model 2600 analyzer, Tekran Inc., Toronto, Ontario) in a class-100 clean room, compliant with US–EPA method 1631. Reagent and analytical blanks were run alongside all samples, the values for which were subtracted from all tissues and standard reference materials.

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MeHg determination of fish tissues and diet

The organic Hg fraction in both fish and invertebrates occupying lower trophic levels is typically less that 100% of THg concentrations (Lasorsa and Allengil 1995; Tremblay and Lucotte 1997; Bowles et al. 2002). Therefore, we determined organic Hg of fish stomach contents to estimate MeHg in fish diets used in this study. Because the majority of organically bound Hg in animal tissues is in the form of MeHg (Paterson et al. 1998), fish tissues and stomach contents were analyzed for organic Hg content to estimate MeHg.

Whole fish (young of the year) or fish tissues (muscle or testes) were homogenized using a stainless steel Polytron homogenizer–sonicator (Brinkman Instruments Inc., Rexdale, Ontario). Samples were homogenized for 10-s intervals and kept on ice between homogenizations to avoid excessive heating. The process was repeated until homogenization was complete. To avoid cross-contamination, we rinsed the blades of the homogenizer thoroughly between samples with a combination of metal-specific detergent (Citranox™) and Hg-free deionized water and then wiped them dry with a clean Kimwipe™. Subsamples of fish tissue homogenates were added to preweighed, acid-washed, 20-mL scintillation vials and weighed (a second set of subsamples of these tissues were also taken for dry-weight and THg determinations). Five millilitres of Hg-free deionized water was added, and samples were again homogenized using clean techniques to avoid cross-contamination.

Wet stomach contents were transferred to 20-mL, preweighed, acid-washed glass scintillation vials, weighed, dried at 50 °C overnight, reweighed, and pulverized with an acid-washed glass rod. To avoid cross-contamination, we rinsed glass rods with a combination of concentrated H_2SO_4 and deionized water and then wiped dry with an Hg-free Kimwipe™. Five millilitres of Hg-free deionized water was added to the ground stomach contents.

After receiving 5 mL of Hg-free deionized water, all samples received 3 mL of 0.65 mol·L^{-1} $CuSO_4$, and 4 mL of 3 mol·L^{-1} KBr. Samples were shaken for 30 min, after which 5 mL of a 3:2 mixture (*v*/*v*) of methylene chloride – hexane was added to extract organically bound Hg from the sample and shaken for 24 h. Samples were allowed to settle overnight. Four millilitres of the organic layer was then removed and added to clean, acid washed digestion tubes. Samples were digested and analyzed for THg as previously described.

Analytical quality assurance and control

National Research Council (NRC) certified biological reference standards DORM-2 and DOLT-2 (http://inms-ienm.nrc-cnrc.gc.ca/calserv/crm_e.htm#data) were analyzed concurrently with tissues for MeHg and THg determinations and corrected for by blank subtraction. Mean raw values of THg for DORM-2 and DOLT -2 over the course of the study (21 replicate digests) were 4.70 μg Hg·g^{-1} dry weight and 2.26 μg Hg·g^{-1} dry weight, respectively, (standard errors: DORM-2, 0.17 μg·g^{-1}; DOLT-2, 0.09 μg·g^{-1}). These values fall within 10% of the reported NRC THg concentrations and within 95% confidence limits reported by NRC (DORM-2 = 4.64 ± 0.26 μg·g^{-1}; DOLT-2 = 2.14 ± 0.28 μg·g^{-1}). Average recoveries for uncorrected DORM-2 and DOLT-2 over the course of the study were 101% and 106%, respectively. Analytical spike recoveries averaged 109%, with one–five spikes run in each analysis over 14 analytical runs. The average value for DORM-2 over all organic Hg analyses over the course of the study (17 replicate digests) was also within 10% of the nominal MeHg concentration reported by NRC (DORM-2 = 4.47 ± 0.32 μg·g^{-1}).

Considerable deviation from the nominal values in NRC standards occurred in 7 of the 21 THg digest runs performed during the study. For analyses where DORM-2 values deviated by more than 15% of nominal values, corrections of fish Hg concentration were made by dividing the observed concentration by a specific run bias correction factor, equal to the ratio of the average observed DORM-2 value in a digest to nominal values reported by NRC. We validated this correction with use of a power analysis, which determined that flesh tissues taken from the same fish run in different digests were indistinguishable from one another after correction (Rennie 2003).

Table 3. Swimming behaviours and associated swimming speeds observed using data collected from both Plastic Lake and Shoe Lake yellow perch (*Perca flavescens*), July 2001.

Behaviour observed	Swimming speed[a]	*N*
Swimming	1.46±0.13	22
Slow-swimming	0.73±0.06	21
Darting	5.25±1.15	6
Hovering (stationary)	0	na

Note: Numbers reported are averages based on data collected from both lakes. na, not applicable.
[a]Body lengths·s^{-1} ± 1 SE.

Observed swimming behaviour

Direct observations of fish were performed between 31 July and 15 August 2001 and between 26 July and 1 August 2002. 2001 data were collected in the morning (0600–1000, local time), afternoon (1000–1700), and evening (1700–2000) from both lakes, whereas 2002 data were collected in late morning – early afternoon only. Lakes were sampled on alternate dates so as to control for potential seasonal or lunar differences between lakes over the sampling period.

A snorkelling observer remained motionless while visually tracking a particular fish. Before timing began, the observer estimated the total length of a chosen fish. The activities of the fish were then documented over a 5-min period of observation. Seven activities for fish were documented; swimming, slow-swimming, chasing, escaping, darting, flashing, and hovering (stationary). Swimming speeds (in body lengths per second) were estimated for swimming, slow-swimming, and darting behaviours from both lakes in 2001 (Table 3). Five to fifteen observations of individual fish were taken from three–four sites around each lake during each time period recorded, as time and daylight permitted. Swimming and slow-swimming were differentiated by the relative speed with which fish were moving; chasing and escaping were characterized by the pursuit of one fish by another, at speeds approximating those observed for "swimming"; darting was noted as a very fast sudden movement, often the result of a startle response or escape from predation. Flashing was noted as a quick change in direction,

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during which fish appeared to scrape up against objects in the water. The swimming speed for flashing was assigned the same value as that for darting.

For each individual fish, we summed the total time spent performing a given behaviour over the 5-min period of observation. Active behaviours were summed to estimate the total amount of time in a 5-min period spent active for an individual fish. Observers also quantified the number of feeding behaviours observed over the 5-min period. Feeding behaviours were classified as fish actively pecking at substrates or at open water (presumably zooplankton). Frequency of feeding behaviours were $\log_{10}(x+1)$-transformed to normalize distributions before analyses.

Energetics calculations using field swimming observations

Hourly energetics of fish were calculated using equations modified from Trudel and Boisclair (1996):

$$E_h = 12 \cdot E_{5\,\mathrm{min}} \quad (12)$$

$$E_{5\,\mathrm{min}} = \sum_{n}^{i} Eb_i 13.56 \quad (13)$$

where E_h is the hourly energetic investment of an observed fish (E·h^{-1}), $E_{5\,\mathrm{min}}$ is the energetic investment in activity of the fish per 5-min period (J·5 min^{-1}), $\sum_n^i Eb_i$ is the sum of energetics for each (ith) behaviour over n behaviours observed, and 13.56 is an oxycaloric value (J·mg O_2^{-1}; Elliott and Davidson 1975). Energetics for individual fish behaviours, Eb_i (mg O_2·min^{-1}), was calculated as

$$Eb_i = O_{\mathrm{cost}(i)} Ts_i \quad (14)$$

where $O_{\mathrm{cost}(i)}$ is the cost of a particular activity (mg O_2·min^{-1}), and Ts_i is the number of swimming seconds observed for that activity (min·5 min^{-1}). Swimming cost was estimated using an empirical relationship of oxygen consumption with mean fish weight (W; g wet) and spontaneous swimming speed (S, cm·s^{-1}; Boisclair and Tang 1993):

$$O_h = 0.117 W^{0.54} S^{1.09} \quad (15)$$

Swimming costs per hour (O_h) were calculated, and specific swimming speeds (in body lengths·s^{-1}; Table 3) were converted to absolute swimming speeds (cm·s^{-1}) through multiplication of specific swimming speeds by the estimated size of the fish (cm) under observation.

Daily energetic investment (J·day^{-1}) was estimated by calculating average weight-specific hourly estimates of active energetic investment (J·g^{-1}·day^{-1}) for morning, afternoon, and evening samples in 2001. Weight was estimated from length–weight relationships in the lakes under study. Daily estimates were weighted according to the number of hours defined by each sampling period, and the total was used to estimate weight-specific averages of energetic investment. Night activity in yellow perch was assumed to account for a negligible component of fish activity based on recorded observations using infrared cameras (N.C. Collins, University of Toronto at Mississauga, 3359 Mississauga Road N., Mississauga, ON L5L 1C6, unpublished data).

LDH and protein analyses

Fish carcasses were kept frozen at –20 °C for 6 months immediately prior to analysis; preservation of tissues at –20 °C immediately after capture has been shown to adequately preserve the LDH enzyme (Sherwood et al. 2002*b*). Muscle samples from fish collected in 2002 were prepared and analyzed for both LDH and protein concentrations as described in Rajotte and Couture (2002).

Estimation of growth rate and life history parameters

Specific growth rates were estimated as described by Ricker (1975):

$$G = \frac{1}{\Delta t} \ln\left(\frac{W_t}{W_0}\right) \quad (16)$$

Collections of female fish in early May 2002 were used to determine age and size at maturity of female yellow perch by estimating the inflection point in a logistic regression between maturity status against age or size at maturity. Samples of male fish under 3 years of age were insufficient to calculate age at maturity and were assigned a value of 2 years of age in both lakes for bioenergetic modelling purposes. This value reflects the provincial average for male yellow perch age at maturity in Ontario (Purchase 2003). Instantaneous mortality rates for each population were estimated from catch curves as the slope of the right-hand tail of the distribution of log abundance versus age, using all fish in each lake collected over 2001 and 2002.

Statistical analyses

Comparisons between lakes of log absolute consumption estimates (C; g·day^{-1}) and log activity costs (R_a, kJ·day^{-1}) obtained from mass balance models were made using the log average body size over the time period modelled as a covariate. This analysis was repeated for both seasonal and annual models of fish C and R_a. This approach allowed simple comparisons of slopes and intercepts (using analysis of covariance, ANCOVA) between the populations investigated. A posteriori comparisons were performed to determine significant differences between lakes, and critical p values were corrected for the number of comparisons performed using sequential Bonferroni corrections where appropriate. All statistical procedures were carried out with SAS (Version 6.12, 1989, SAS Institute Inc., Cary, North Carolina). These relationships were used to estimate C and R_a for a 40-g fish, as this size approximates the median size of fish encountered in our experiment and allowed relevant comparisons between lakes from ANCOVA models. Maintenance ration was estimated as the intercept of the relationship between specific consumption rate (day^{-1}) and growth rate (day^{-1}) and can be interpreted as the energy intake required to maintain basic bodily functions without growth or mass loss. Differences between lakes were determined using ANCOVA, after verifying that slopes were not significantly different.

Time spent active, feeding behaviours, and hourly energetic estimates from 2001 swimming observations were compared between lakes across three sampling periods (morning, afternoon, and evening) using analysis of variance (ANOVA). A posteriori comparisons were made using effect coding and hypothesis testing in SAS (SAS Institute Inc.).

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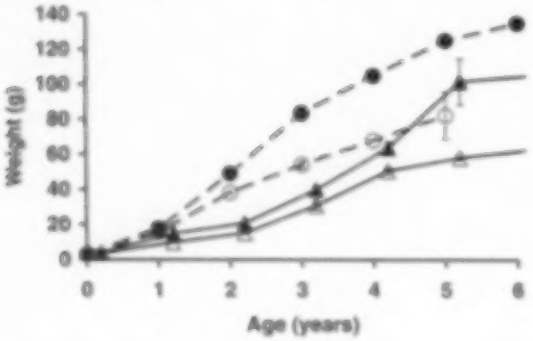
Fig. 1. Yellow perch (*Perca flavescens*) growth (represented by size-at-age of fish collected in August–September 2001–2002) in Plastic Lake (triangles, solid lines) and Shoe Lake (circles, broken lines). Plastic Lake data are offset in time slightly for clarity. Males are open symbols, females are closed symbols. Error bars are ±1 standard error. Projections of lines to age 6 are based on small ($N = 1$) sample sizes or estimated from catch data in May and July.



Observed activity rates for 2002 samples were compared using Student's *t* test. The relationship of muscle LDH activity with body weight was compared between lakes using a test for heterogeneity of slopes.

Results

Growth and life history traits

Size at age was typically greater for Shoe Lake fish for both males and females (Fig. 1). Specific growth rates of perch from Plastic Lake were almost half of those observed in Shoe Lake (*t* test, $t_{13} = 2.87$, $p = 0.013$; Table 4). Female perch from Plastic Lake matured later and were larger than Shoe Lake perch (Table 4). Instantaneous mortality rates were slightly higher in Shoe Lake, but not significantly (test for heterogeneity of slopes, $F_{[1,5]} = 1.01$, $p = 0.36$; Table 4).

Prey availability

The total density of benthic invertebrates collected in Shoe Lake was consistently higher over three sample periods than that in Plastic Lake (Table 2). However, this difference was nonsignificant on average because of high interseasonal variation within a lake and a small sample size (paired *t* test, $t_2 = -2.6$; $p = 0.12$). In contrast, we observed no consistency in differences of the proportion of perch collected with empty stomachs between Shoe and Plastic lakes over the four sampling periods examined, and differences between lakes were not significant (paired *t* test, $t_4 = 0.76$, $p = 0.5$; Table 4).

Bioenergetics estimates

Slopes of log activity costs against log body weight were not significantly different between lakes (test for heterogeneity of slopes: $F_{[1,15]} = 0.6689$, $p = 0.43$). Differences in activity costs between lakes bordered on significant ($p = 0.097$). Activity was generally higher in Plastic Lake perch compared with those in Shoe Lake at small and large body sizes, with considerable overlap for intermediate-sized fish (Fig. 2*a*; Table 5). Residuals from relationships between activity multipliers with body weight were compared between sexes, but no significant difference was detected ($t_{15} = 1.026$, $p = 0.327$).

Table 4. Comparison of yellow perch (*Perca flavescens*) growth, proportion of empty stomachs, and life history traits from the two lakes under study.

Attribute	Plastic Lake	Shoe Lake
Average % of empty stomachs	45.7±10.3	39.2±5.6
Specific growth rate (day^{-1})	0.00248*±0.0007	0.00492±0.0004
Female age at maturity (years)	4.4	3.0
Female size at maturity (mm)	176	166
Maximum age (years)	7	6
Survivorship ($year^{-1}$)	0.47	0.54

Note: Significant differences between lakes are marked with an asterisk.

Slopes of log relative consumption against log body weight were not significantly different between lakes (test for heterogeneity of slopes: $F_{[1,15]} = 1.36$, $p = 0.26$). Estimates of consumption rates were significantly higher in Plastic Lake perch than those in Shoe Lake (Fig. 2*b*; Table 5). Residuals from relationships between consumption and body weight were compared between sexes, but no significant difference was found ($t_{15} = 0.841$, $p = 0.414$). Maintenance ration was estimated to be slightly higher for Plastic Lake perch (0.0458 day^{-1}) than for Shoe Lake perch (0.0352 day^{-1}), though these differences between lakes were not significant ($F_{[1,14]} = 1.14$, $p = 0.3$; Fig. 2*c*).

Swimming observations

Perch in Plastic Lake were typically more active than perch in Shoe Lake (Figs. 3*a*, 3*b*). For 2001 samples, both energetic estimates (joules per gram per hour) and the time spent active over a 5-min period were higher for perch from Plastic Lake than from Shoe Lake (Table 5). Differences between time of collection were also significant ($F_{[2,87]} = 14.16$, $p = 0.0001$). A posteriori comparisons revealed that differences between lakes were significant for morning and afternoon samples, but not for evening samples (morning: $F_{[1,87]} = 10.75$, $p = 0.0001$; afternoon: $F_{[1,87]} = 8.77$, $p = 0.0015$; evening: $F_{[1,87]} = 1.96$, $p = 0.17$; $p_{crit} = 0.01$). Differences between lakes were also observed in 2002 (*t* test, $t_{60} = 4.24$, $p = 0.0001$). Daily energetic estimates (joules per day) based on observed swimming were on average 51% of activity rates calculated from bioenergetics models.

Frequency of perch feeding behaviours observed in a 5-min period was significantly higher for Plastic Lake than for Shoe Lake perch (Fig. 3*c*) and differed by time of sampling ($F_{[2,87]} = 4.22$, $p = 0.0178$). Frequency of perch feeding behaviours in 2002 was not significantly different between lakes ($t_{60} = 0.79$, $p = 0.43$).

Muscle LDH activity

Because LDH is often found to scale positively with body size (Childress and Somero 1990), we selected a narrow range (34–67 g) of body sizes for comparison between lakes

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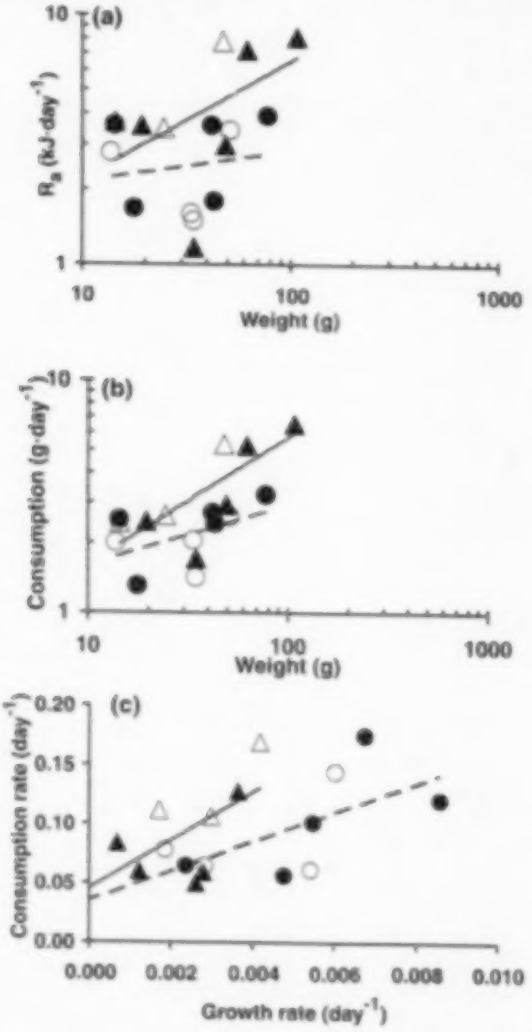
Fig. 2. Bioenergetics of yellow perch (*Perca flavescens*) from Shoe Lake (circles) and Plastic Lake (triangles). Male fish are open symbols, females are solid symbols. Activity costs (R_a) against size (*a*), absolute consumption rates against body size (*b*), and relationships of specific consumption rate with specific growth rate (*c*) are shown.



across both sexes. This size range represents a large proportion (30%–45%) of fish caught in both lakes over the duration of the experiment. Within this size range, Plastic Lake perch had significantly higher muscle LDH activity than Shoe Lake perch (Table 5). We further examined the relationship between enzyme activity and body size for each lake. Shoe Lake muscle LDH activities scaled positively with body size, whereas no relationship was detected in Plastic Lake perch (Fig. 4). A test for heterogeneity of slopes between lakes revealed a significant interaction between perch size and muscle LDH activity (Table 5). The gender of perch did not explain any of the variation in muscle LDH activity.

Sherwood et al. (2002*a*) reported a strong positive relationship between muscle LDH activity and activity expressed as a multiple of standard metabolism. Using means of muscle LDH activity for Plastic Lake and Shoe Lake perch from the 34- to 67-g size range and the equation reported by Sherwood et al. (2002*a*), Shoe Lake perch were estimated to have activity costs 22%–29% lower than Plastic Lake perch. This estimated difference is only slightly lower than differences based on bioenergetics calculations and observed swimming behaviour (Table 5).

Discussion

Multiple independent methods of assessment agree that both activity levels and consumption rates are higher in Plastic Lake than in Shoe Lake. For activity level, two tests show significant differences at the 5% level and one at the 10% level; consumption rates were different at the 5% and 0.1% level. Since these are independent data testing the same scientific hypothesis (i.e., that slow-growing Plastic Lake fish act and feed differently than Shoe Lake fish), we combined these probabilities to determine the overall significance across all experiments (Sokal and Rohlf 1995). Activity differences between the two lakes were highly significant when *p* values were combined across all three methods (χ^2_6 = 28.04, $p < 0.0001$). Consumption rates were also highly significant across both methods of estimation (χ^2_4 = 20.69, p = 0.0004). Therefore, we conclude that the evidence for differences in both activity and consumption between the lakes is very strong, with both activity and consumption being significantly higher in Plastic Lake.

Our data illustrate that slow growth in Plastic Lake perch is a direct consequence of higher activity rates in this population, despite much higher rates of energy uptake (consumption) in Plastic Lake perch compared with Shoe Lake perch. Averaging across all methods of estimation, feeding rates of fast-growing Shoe Lake perch were 45% lower than slow-growing Plastic Lake perch, and activity costs were 28% lower in Shoe Lake perch compared with the slow-growing population of Plastic Lake. How lower activity and consumption combine to result in faster growth may at first seem counterintuitive. It may be that this demonstrates a greater effect of activity levels over consumption in determining overall growth rates; the energy saved by Shoe Lake perch by not allocating to activity may more than make up for reduced feeding rates. This pattern is also perhaps a reflection of the design of the BM, since the allometric exponent for metabolic activity (0.8) is greater than the allometric exponent for C_{max} for perch (0.72, Kitchell et al. 1977; Hewett and Johnson 1992). Thus, for the same size of fish, a decrease in active metabolism will result in a greater amount of excess energy (and thus growth, as it is defined in the BM) than would an equal proportional increase in consumption. Clearly, more data is required to address these possibilities directly. Regardless, the clear implication from our findings is that Plastic Lake fish are left with a lower rate of net energy available for growth because of higher activity costs, despite higher feeding rates.

The general agreement among these three independent estimates of activity costs helps support the use of bioenergetics approaches to determining activity costs in the

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Table 5. Statistical summary of various consumption and activity estimation methods between Shoe Lake and Plastic Lake yellow perch (*Perca flavescens*).

Variable	Estimation method	Test statistic	p	% difference	Figure
Consumption	Bioenergetics	$F_{[1,34]} = 5.67$*	0.0321*	33.1[a]	2*b*
	Observed feeding behaviour	$F_{[1,87]} = 11.60$*	0.001*	57.7[b]	3*c*
Activity (R_a)	Bioenergetics	$F_{[1,34]} = 3.16$	0.097	39.7[a]	2*a*
	Observed swimming behaviour	$F_{[1,87]} = 14.31$*	0.0003*	37.1[b]	3*b*
Activity (physiological anaerobic capacity)	Differences in LDH activity for fish 34–67 g	$t_{40} = 2.04$*	0.028*	10.2	4
	LDH activity across observed size range of fish	Lake×weight interaction: $F_{[1,81]} = 9.57$*	0.0027*	na	4

Note: Significant statistical results are marked with an asterisk. Percent difference is calculated as the difference between lakes divided by the value observed in Plastic Lake, expressed as a percentage. LDH, lactate dehydrogenase; na, not applicable.

[a]At 40 g.

[b]Average of four time periods.

Fig. 3. Time spent active over a 5-min period of observation (*a*), estimates of relative energy expenditure per hour calculated from observed behaviour of individual yellow perch (*Perca flavescens*) over a 5-min period (*b*), and comparison of feeding behaviour (*c*) for yellow perch in Plastic Lake (triangles, solid line) and Shoe Lake (circles, broken line). Solid symbols are 2001 data, open symbols are 2002. 2002 samples were collected over late morning – early afternoon. Error bars are ±1 standard error.

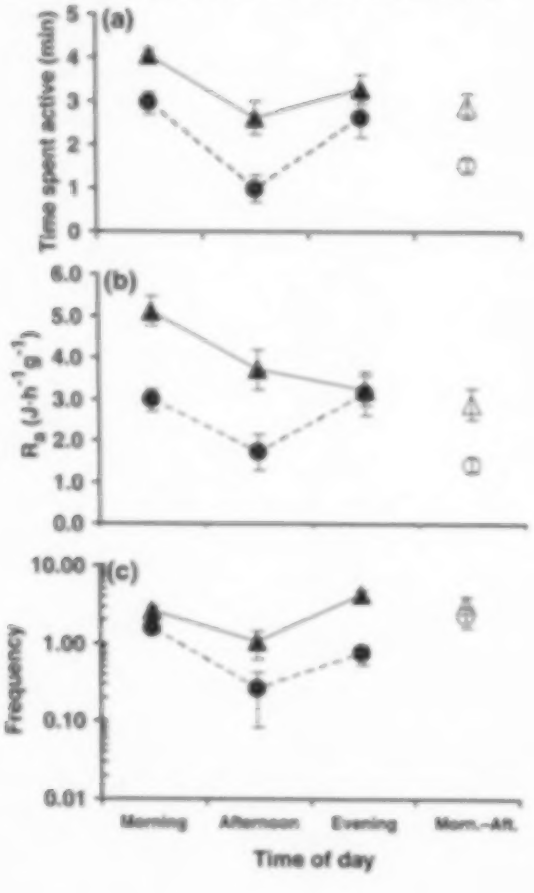
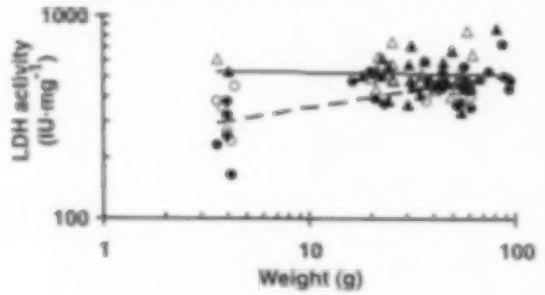


Fig. 4. Relationship between lactate dehydrogenase (LDH) activity and body size for yellow perch (*Perca flavescens*) collected in Plastic Lake (triangles, solid line; $F_{[1,43]} = 0.06$, $p = 0.81$) and Shoe Lake (circles, broken line; $F_{[1,38]} = 33.22$, $r^2 = 0.47$, $p < 0.0001$). Males are open symbols, females are solid symbols.



field. A number of studies have used contaminant–bioenergetic approaches to determine that activity costs were important determinants of growth and life history of fish (Trudel et al. 2001; Pazzia et al. 2002). These studies use field-validated contaminant bioaccumulation models to estimate fish consumption (Rowan and Rasmussen 1996; Trudel et al. 2000). However, activity costs determined using this approach have not been compared with alternate methods in wild populations. Though the results in this paper do not truly constitute a validation of the contaminant–bioenergetics approach, as none of the methods can be said to represent an absolute measure of activity in our populations, the close convergence of three independent methods argues that the pattern observed is very likely real and not simply an artefact of our estimation methods. Given that the qualitative differences between populations are real, as the combined statistical assessments clearly demonstrate, then an additional finding of our study is that the statistical power of the contaminant–bioenergetics approach to detect differences in activity is low compared with the two other methods we employed; only relatively large differences in activity derived from the contaminant–bioenergetics approach are likely to be detectable. A necessary corollary of this finding suggests that when statistically significant differences between populations are detected using this method, then the true effect is likely to be much stronger than the statistical probability indicates,

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relative to the other methodologies employed in this study. This demonstration of the relatively conservative nature of the contaminant–bioenergetics approach in estimating differences in activity costs should lend additional support to studies employing this methodology that do report significant (or close to significant) differences in field-based activity costs between populations.

The trade-off between realized growth rates and activity in fish has long been recognized (Weatherly 1966; Boisclair and Leggett 1989*b*), but to our knowledge, only one other study has formally examined this relationship between natural populations in their native habitat using multiple independent methods for determination of activity costs. Aubin-Horth et al. (1999) reported that young-of-the-year perch from a fast-growing lake allocated a lower percentage of their total energy budget to activity than those in a lake with slower growth. However, the generality of the findings from this study are unclear, as the fish examined were limited to body sizes less than 10 g and differences in activity were low relative to the range of growth observed between the two populations under study. Our study independently supports the suggestion of Aubin-Horth et al. (1999) of a negative relationship between growth and activity in yellow perch, using multiple independent methods of assessing activity costs. Additionally, our study demonstrates that this relationship also applies to fish of larger body sizes and that the observed differences in activity costs between our populations are as large as has been observed elsewhere in nature (Boisclair and Leggett 1989*b*).

Neither of the populations considered in this study appear to suffer from starvation, given that the number of empty stomachs between lakes was roughly equivalent. As well, food availability (based on consistently higher patterns of benthic invertebrate density) appears to be higher overall in Shoe Lake. Perch in Plastic Lake may therefore need to increase their level of activity to seek out sufficient energy for growth and reproduction. It is possible that the absence of predators in Plastic Lake allows these perch to allocate a greater amount of energy to foraging activities than one might observe otherwise, since the risk of predation is much lower in Plastic Lake than in Shoe Lake. Similarly, one could argue that activity levels are essentially capped in Shoe Lake because of the presence of large-bodied piscivores. If food sources were to become limiting in this lake, an increase in activity might lead to a greater exposure of perch to large-bodied predators and thus reduce the number of active individuals. From this perspective, a trait-mediated "positive" effect of predator presence (Abrams 1984) may be contributing to higher growth rates in Shoe Lake perch. Positive trait-mediated effects of predators on prey have been well documented experimentally (Peacor 2002).

Given a fixed mortality rate, life history models (Roff 1984; Lester et al. 2004; Shuter et al. 2005) predict that slower growth will be associated with later maturity. This prediction is consistent with our observations, since both populations exhibited similar mortality rates and yet the slower-growing population (Plastic Lake) matured 1 year later than the faster-growing population. A similar result is predicted when maturity is assumed to occur at constant size, which does not appear to be the case for yellow perch. Though size at maturity is not dramatically different between our two populations, recent studies of yellow perch in Ontario have demonstrated two- to three-fold differences among populations in mean female size at maturity and age at maturity (Purchase et al. 2005), concluding that females of this species do not mature at a fixed size or age. In contrast with our findings, other studies (Ridgway and Chapleau 1994; Jansen 1996; Claramunt and Wahl 2000) have found that slower growing or stunted populations tended to mature earlier than faster-growing populations. However, in these studies it was either estimated or assumed that slow growth was associated with higher mortality (Jansen 1996; Claramunt and Wahl 2000; Trudel et al. 2001), thus leading to a decline in age at maturity (Roff 1984). This is in contrast with our two populations, where estimated moralities were similar.

Sexual dimorphism in growth was also observed in these lakes. Owing to their smaller size at age, one might also expect male perch to either eat less or be more active. However, there appeared to be no consistent or systematic variation between sexes in either consumption or active metabolism that could explain between-sex differences in growth in our two populations. This is in contrast with recent work that detected significant differences between activity and consumption rates in sexually dimorphic walleye from Ontario (Henderson et al. 2003). Because differences in size and Hg concentrations between populations (lakes) at a given age in this study are much larger than those between sexes within a population, we may not have had adequate statistical power to resolve between-sex differences in consumption and activity.

Overall, our results support the validity of the contaminant–bioenergetic approach to estimating activity and add to the small body of literature suggesting that among-lake variation in activity costs are at least as important as variation in food consumption in determining the growth rates of freshwater fish populations. The contaminant–bioenergetic approach, though perhaps conservative relative to other methods, is easy to employ in the field and to apply to archived data. We hope this study encourages further use of the contaminant–bioenergetics approach in studies of activity levels and their variation across fish populations.

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Appendix A

Appendix appears on the following page.

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Table A1. Summary of body weight (W), Hg concentrations in fish (Hg), methylmercury (MeHg) concentrations in food (C_d), consumption rates (C), activity cost (R_a), and activity multipliers (ACT) for fish calculated using the Hg mass balance model combined with a bioenergetics model.

Year modelled	Age	Sex	Maturity	W_0 (g)	W_t (g)	Hg_0 ($\mu g \cdot g^{-1}$)	Hg_t ($\mu g \cdot g^{-1}$)	C_d ($\mu g \cdot g^{-1}$)	C (day^{-1})	R_a ($kJ \cdot day^{-1}$)	ACT
Plastic Lake											
2001	2	1	1	11.72	15.26	0.150	0.149	0.013	0.169	3.70	4.57
				(0.32, 20)	(0.41, 34)	(0.006, 20)	(0.011, 26)	(0.004, 43)	(0.024)	(0.60)	(0.56)
2002	3	1	1	22.16	26.76	0.211	0.177	0.017	0.106	3.53	3.14
				(0.67, 33)	(1.20, 27)	(0.024, 10)	(0.012, 10)	(0.002, 22)	(0.031)	(1.47)	(0.88)
2002	4	1	1	44.97	50.11	0.219	0.196	0.015	0.112	7.80	3.77
				(1.08, 6)	(2.26, 7)	(0.012, 6)	(0.012, 6)	(0.002, 18)	(0.029)	(2.48)	(0.87)
2001	2	2	0	16.39	20.63	0.137	0.129	0.013	0.128	3.61	3.74
				(0.27, 139)	(0.72, 60)	(0.005, 39)	(0.007, 42)	(0.004, 43)	(0.018)	(0.68)	(0.49)
2001	3	2	0	43.79	52.22	0.156	0.190	0.043	0.060	3.01	2.09
				(1.78, 40)	(3.21, 12)	(0.007, 26)	(0.020, 10)	(0.023, 28)	(0.013)	(1.29)	(0.46)
2002	3	2	0	31.63	37.29	0.177	0.130	0.017	0.050	1.16	1.54
				(0.77, 63)	(1.19, 55)	(0.013, 10)	(0.006, 12)	(0.002, 22)	(0.017)	(1.19)	(0.55)
2002	4	2	1	60.84	63.48	0.177	0.165	0.015	0.084	7.25	3.08
				(1.75, 19)	(4.02, 6)	(0.012, 10)	(0.016, 6)	(0.002, 18)	(0.035)	(4.06)	(1.15)
2001	5	2	1	101.30	109.30	0.215	0.254	0.044	0.060	8.20	2.58
				(6.58, 5)	(12.35, 6)	(0.027, 5)	(0.106, 2)	(0.032, 3)	(0.041)	(7.95)	(1.51)
Shoe Lake											
2001	1	1	0	10.70	15.67	0.091	0.097	0.012	0.144	2.77	3.70
				(0.55, 25)	(0.51, 16)	(0.006, 16)	(0.012, 16)	(0.002, 28)	(0.030)	(0.18)	(0.73)
2001	2	1	1	27.30	38.47	0.123	0.116	0.027	0.061	1.59	1.77
				(1.18, 5)	(0.76, 46)	(0.009, 5)	(0.004, 27)	(0.011, 38)	(0.008)	(0.11)	(0.23)
2002	2	1	1	31.17	37.32	0.118	0.114	0.019	0.064	1.49	2.12
				(0.93, 13)	(1.28, 5)	(0.006, 10)	(0.004, 5)	(0.002, 15)	(0.009)	(0.09)	(0.28)
2002	3	1	1	48.16	54.23	0.151	0.168	0.024	0.078	3.44	2.86
				(2.61, 15)	(2.09, 8)	(0.006, 10)	(0.012, 8)	(0.003, 29)	(0.015)	(0.22)	(0.50)
2001	1	2	0	10.78	16.52	0.089	0.108	0.012	0.175	3.59	4.39
				(0.46, 28)	(0.63, 19)	(0.005, 14)	(0.019, 13)	(0.002, 28)	(0.038)	(0.22)	(0.84)
2002	1	2	0	13.00	22.37	0.068	0.104	0.019	0.120	1.66	3.23
				(0.72, 10)	(2.25, 6)	(0.004, 10)	(0.011, 6)	(0.001, 16)	(0.019)	(0.99)	(0.53)
2001	2	2	0	36.30	49.07	0.124	0.116	0.027	0.056	1.79	1.70
				(1.98, 26)	(1.15, 82)	(0.005, 19)	(0.004, 57)	(0.011, 38)	(0.007)	(0.11)	(0.19)
2002	2	2	0	35.01	49.48	0.101	0.122	0.019	0.101	3.59	3.33
				(1.58, 10)	(3.04, 12)	(0.006, 9)	(0.004, 9)	(0.002, 15)	(0.010)	(0.11)	(0.30)
2002	3	2	1	71.81	83.46	0.127	0.140	0.024	0.065	3.92	2.53
				(4.36, 8)	(3.96, 24)	(0.006, 8)	(0.012, 10)	(0.003, 29)	(0.014)	(0.32)	(0.52)

Note: Values in parentheses are standard errors and the number of observations used to calculate means, respectively. For sex, 1 is male, 2 is female. For maturity, 0 is immature, 1 is mature.

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Life history trade-offs and community dynamics of small fishes in a seasonally pulsed wetland[1]

Donald L. DeAngelis, Joel C. Trexler, and William F. Loftus

Abstract: We used a one-dimensional, spatially explicit model to simulate the community of small fishes in the freshwater wetlands of southern Florida, USA. The seasonality of rainfall in these wetlands causes annual fluctuations in the amount of flooded area. We modeled fish populations that differed from each other only in efficiency of resource utilization and dispersal ability. The simulations showed that these trade-offs, along with the spatial and temporal variability of the environment, allow coexistence of several species competing exploitatively for a common resource type. This mechanism, while sharing some characteristics with other mechanisms proposed for coexistence of competing species, is novel in detail. Simulated fish densities resembled patterns observed in Everglades empirical data. Cells with hydroperiods less than 6 months accumulated negligible fish biomass. One unique model result was that, when multiple species coexisted, it was possible for one of the coexisting species to have both lower local resource utilization efficiency and lower dispersal ability than one of the other species. This counterintuitive result is a consequence of stronger effects of other competitors on the superior species.

Résumé : Nous avons utilisé un modèle unidimensionnel spatialement explicite pour simuler la communauté des petits poissons dans des terres humides d'eau douce du sud de la Floride, É.-U. La variation saisonnière des précipitations dans ces terres humides produit des fluctuations annuelles de la surface inondée. Nous avons modélisé des populations de poissons qui diffèrent entre elles seulement par l'efficacité de leur utilisation des ressources et par leur pouvoir de dispersion. Les simulations montrent que ces compromis, alliés à la variabilité temporelle et spatiale de l'environnement, permettent la coexistence de plusieurs espèces qui sont en compétition d'exploitation pour le même type de ressources. Ce mécanisme est inusité dans son détail, bien qu'il partage quelques caractéristiques avec d'autres mécanismes proposés pour expliquer la coexistence d'espèces compétitrices. Les densités de poissons dans les simulations ressemblent aux patrons de densité observés dans les données empiriques provenant des Everglades. Les cellules dont l'hydropériode dure moins de six mois accumulent des quantités négligeables de biomasse de poissons. Un résultat exceptionnel de la modélisation est que, lors de la coexistence de plusieurs espèces, il est possible pour l'une des espèces en présence de posséder à la fois une efficacité d'utilisation des ressources locales et un pouvoir de dispersion plus bas que ceux d'une autre des espèces. Ce résultat à première vue illogique est la conséquence des effets plus importants d'autres compétiteurs sur les espèces de niveau supérieur.

[Traduit par la Rédaction]

Introduction

Fishes are the most abundant vertebrates in the Everglades and Big Cypress wetland ecosystems of southern Florida. Small-bodied species, composed particularly of about 10 species of livebearers (poeciliids) and killifishes (cyprinodontids and rivulids) having similar life cycles and resource use, dominate the community by numbers. They constitute an ecosystem component whose biomass is the major energy resource for higher trophic levels, especially wintering and breeding wading birds (Ogden 1994; Crozier and Gawlik 2003). Systematic, human-induced changes in hydrology over the last several decades have altered hydroperiods in most wetland areas, thereby diminishing this fish forage base or changing the pattern of its availability. Lack of sufficient biomass and availability of prey is hypothesized to have been a major factor in the decline of wading bird nesting at traditional Everglades' rookeries (Ogden 1994). Recovery of historic fish patterns is a primary goal for restoration of southern Florida wetlands (Ogden et al. 2003).

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D.L. DeAngelis,[2] US Geological Survey, Florida Integrated Science Center, Department of Biology and Biological Resources Division USGS, University of Miami, P.O. Box 249118, Coral Gables, FL 33124, USA.
J.C. Trexler. Department of Biological Sciences, Florida International University, Miami, FL 33199, USA.
W.F. Loftus. US Geological Survey, Florida Integrated Science Center, Everglades National Park Field Station, Homestead, FL 33043, USA.

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[2]Corresponding author (e-mail: ddeangelis@bio.miami.edu).

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The strongly seasonal rainfall pattern of this region creates a cycle of wet and dry seasons. Because of the flat landscape, relatively small differences in mean water level amplify into large differences in the amount of wetted area and flooding duration, which affect many plant and animal communities. The wetland small-fish community is strongly influenced by seasonal hydrologic fluctuations (Loftus and Kushlan 1987; Trexler et al. 2002).

The coexistence of many fish species of similar small body size and resource use begs for an explanation (Strange and Foin 1999). Our operating hypothesis is that fluctuations in available habitat, along with trade-offs in life history traits, play key roles in maintaining this community. As vast areas of wetland are reflooded each year, opportunistic fish species can disperse into and exploit those areas first, while other species appear to be better at dominating more permanently inundated areas of marsh. Species better at exploiting more stable areas should have higher reproductive and (or) survival rates in long-hydroperiod areas, and they should be slower to disperse.

Materials and methods

We hypothesize that maintenance of a diverse wetland fish community can be related to current ecological theory on nonequilibrium communities. Environmental fluctuations are often proposed as a means for maintaining richness in a dynamic community by preventing competitively dominant species from eliminating others. Chesson (2000) reviewed the mathematical models showing that environmental fluctuations could promote diversity in nonequilibrium communities, when the fluctuations effectively provide distinct niches for the competing species. These circumstances may occur when the competing species have trade-offs in key physiological and (or) behavioral traits that allow the relative advantages to alternate among species in a fluctuating environment.

One type of nonequilibrium model is that of Litchman and Klausmeier (2001). That model was based on trade-offs in coexisting species, phytoplankton species in their case, competing under seasonally periodic light availability. One species (opportunist) was able to grow faster under initially high levels of light, but when phytoplankton biomass increased to the point that self-shading occurred, the advantage shifted to the other species (gleaner). Both species declined during the period of the year when external solar radiation was low. For certain ratios of light to dark period, coexistence was possible. The opportunist–gleaner species trade-off is a useful idea, although in the Everglades fish community, spatial movement probably plays a role, as in "successional mosaic" models (Armstrong 1976; Tilman 1994; Holmes and Wilson 1998). In that hypothesis, disturbances occur asynchronously across the landscape, creating new habitats ready to be recolonized. If some members of the regional species pool have traits that allow invasion of newly available gaps where they increase rapidly, while others invade slowly but are better competitors and eventually displace the pioneers, species diversity can be maintained. Areas within this dynamic landscape offer a range of successional stages at a given time, allowing niches for many different life history traits. Other models of this class assume that all patches are continuously occupied by all the species, but differences in dispersal rates, along with differences in resource growth rates on different patches, can maintain more than one species on a given resource (Abrams and Wilson 2004; Namba and Hashimoto 2004).

Our conceptual model for the South Florida wetland fish community contains the primary elements, resource fluctuations and spatial dispersal, of the above nonequilibrium hypotheses. However, the mechanism that we propose differs slightly from each of those. As in the successional mosaic hypothesis, fish species populations move at different rates into newly opened (flooded) habitat, with the more competitive species moving more slowly than the more opportunistic ones. But this recolonization process does not occur in randomly and asynchronously opened habitat patches, as in gap creation in forest systems, but as large annual pulses during the seasonal flooding period. In addition, during the dry season, the recession of water forces all populations together into permanent or semipermanent waterbodies.

The gradual opening of new habitat by the rising water gives the more effectively dispersing fish species a temporary advantage during which they can build in numbers before being subjected to competition by the other invaders. When the waters recede, the opportunistic fish are subjected again to heavy competition, but if they have built up high enough numbers, the species may persist. This mechanism can be demonstrated mathematically for very simple cases. Consider two competing fish species, Species 1 and 2, that can occupy two spatial areas, Regions 1 and 2, one of which (Region 1) is continually flooded, while Region 2 floods seasonally for several months. The two fish species differ as follows. Species 1 has greater resource use efficiency and hence can outcompete Species 2 when both are present in either region but is a less efficient disperser, so only a small proportion of the Species 1 population invades Region 2 during the time that it is flooded. A large fraction of Species 2 invades Region 2 when it is flooded.

It is essential also to assume that both species have carrying capacities in each region. It can be shown mathematically that the two species can coexist over a range of parameter values. Here, we will only show one numerical simulation of a simple differential equation model of Species 1 and Species 2, which inhabit Region 1 continuously and alternately disperse into and out of Region 2 as it floods and dries out. An example of the trajectories of the two species in the two regions is shown (Fig. 1, details given in the legend). As a result of its numerical head start in the seasonally flooded area, the poorer competitor is able to build to high enough numbers to persist, despite being outcompeted in both the permanently flooded region and the seasonally flooded region.

It is possible to extend the mathematical model to describe the coexistence of more fish species. Instead, we chose the alternative of using a more detailed simulation model to support our hypothesis. This allows inclusion in the model of aspects of the wetland fish community, such as age and size structure, that are important for the results to be believable.

Simulation model development

We developed a spatial model of a community of age- and size-structured fish species. This model, ODFISH (one-dimensional fish model), simulates a fish community along a

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Fig. 1. Plots of the biomasses of the hypothetical Species 1 and 2 from a two-species, two-region Lotka–Volterra competition model, where Region 1 is continuously flooded and Region 2 is flooded for part of the year. In both regions, the intrinsic growth rates for the two species are $r_1 = 0.208\text{-day}^{-1}$ and $r_2 = 0.204\text{-day}^{-1}$, while the coefficients of competition and self-regulation are $c_{11} = c_{22} = c_{12} = c_{21} = 0.2\text{-day}^{-1}$. One half of the population of Species 2, but only 0.05 of the population of Species 1, move to Region 2 on day 110 (start of flooding of Region 2) and one half of both populations survive on day 240 (end of flooding of Region 2) to move back to Region 1. No further movement takes place between the regions besides those days. Biomass of Species 1 is represented by the thick solid line (Region 1) and thick broken line (Region 2). Species 2 is represented by the thin solid line (Region 1) and thin broken line (Region 2).

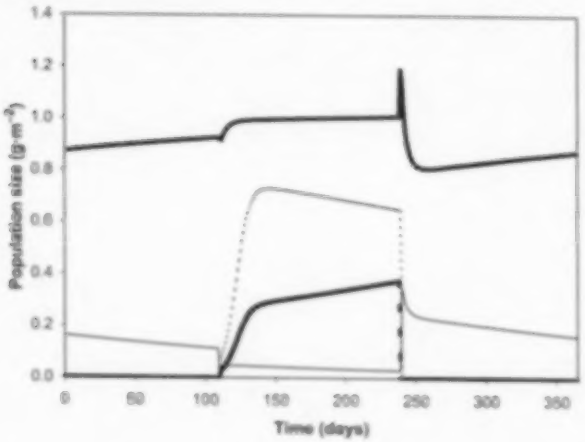
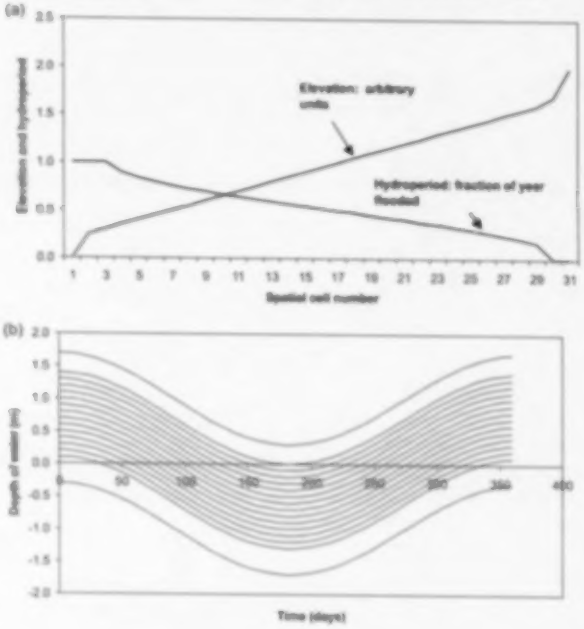


Fig. 2. Description of the physical characteristics modeled. (*a*) Elevation and resultant hydroperiod of each cell along the one-dimensional transect. (*b*) Seasonal pattern of water depths of 16 of the total of 32 spatial cells (the others are spaced between these lines). The extreme upper and lower curves correspond to the continually flooded and continually dry cells, Cells 1 and 32, respectively. The hydroperiods of the other cells lie in between these.



one-dimensional elevation gradient by modeling the fish community dynamics in a sequence of spatial cells along the gradient. As elevation increases along the gradient, the hydroperiods of individual spatial cells decrease. The model has two trophic levels, fish and a single common food resource.

We applied ODFISH to small fishes representative of the Everglades. Our first objective was to determine the reasonableness of the model in simulating the dynamical patterns in space of a single fish population. The second objective was to determine if the mechanism involving trade-offs between traits for resource use efficiency and dispersal is plausible for explaining maintenance of coexistence of species utilizing a common resource.

The model ODFISH is based on an earlier model developed for the small-fish community of southern Florida, the single-spatial cell fish fodel (DeAngelis et al. 1997). The single-cell fish model describes the dynamics of the functional group of small freshwater fish in an area uniform in elevation. ODFISH extends this model to several competing species of small fishes in a one-dimensional series of cells along an elevation gradient. One simplification of the single-cell model is ignoring refugia (e.g., alligator ponds) within spatial cells, which are present in the original unit cell model, in order on a smaller number of mechanisms for coexistence. ODFISH is a simulation model, not an analytic model. It is designed to approximate the sort of dynamics that should occur in a population of small fishes in an expanding and contracting floodplain in more detail than an analytic model can achieve. Details such as population age and size structure make explanation of results more difficult than in simple analytic models. But the mechanism of coexistence described in the preceding section (Fig. 1) is explicitly present in ODFISH. That is, ODFISH incorporates the trade-off between local competition and dispersal.

Physical environment

ODFISH simulates an elevation gradient by a one-dimensional array of 32 cells, starting from Cell 1, which was always flooded, to Cell 32, which was always dry for the range of water levels simulated. The elevation of cells increases linearly from Cell 1 to Cell 32 (Fig. 2*a*). Each cell is 250 m × 250 m, internally homogeneous, and characterized by a mean elevation. This size is small enough to provide good spatial resolution, as there is only about a 6-cm difference in elevation between adjacent cells but large enough that each cell can contain a sizable population of small fishes.

The water depth (water level relative to the cell elevation) of the spatial cells is simulated by a sinusoidal function within each year (Fig. 2*b*). Water levels change on daily time steps. This results in a truncated sinusoidal change in water depth for each cell, with the period of flooding decreasing with the elevation of the cell.

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Table 1. Main parameter values of ODFISH (one-dimensional fish model).

Length of spatial cell		250 m
Lower trophic level productivity	Input	0.8 g dry weight·m^{-2}·day^{-1}
Turnover rate of lower trophic level biomass	m	0.5·day^{-1}
von Bertalanffy growth coefficients	L_∞	4.5 cm
	K	0.015·day^{-1}
	s_0	6.0 days
Assimilation coefficient	a	0.5
Length–weight coefficients	α_1	0.00128
	α_2	3.02
Survival coefficients	F_b	0.04 g dry weight·m^{-2}
	F_p	0.05·day^{-1}
	F_a	0.004·day^{-1}

Food resources

The food resources, R, for the fish in each cell are described by a differential equation similar to the resource dynamics of a chemostat:

$$\frac{dR}{dt} = \text{input} - mR - \text{loss to fish}$$

where input is a constant rate of productivity, mR represents losses not related to consumption by fish, and loss to fish corresponds to removal of resource by fish that is translated into fish population biomass growth. Lower trophic level productivity and turnover rates were parameterized to resemble typical values in southern Florida wetlands (values in Table 1).

Fish life cycles

The fish species represented in ODFISH are small omnivorous fishes that include, for example, eastern mosquitofish (*Gambusia holbrooki*), flagfish (*Jordanella floridae*), and other cyprinodontiform fishes common in the Everglades and Big Cypress Swamp (Loftus and Kushlan 1987). We simulated growth and mortality in age-classes on 1-day time steps, but reproduction only occurred on 10-day steps. At age s, the size of the fish (length L) was given by a von Bertalanffy equation:

$$L_s = L_\infty\{1 - e^{-K(s - s_0)}\}$$

Weight (W) in grams dry weight is given by the weight–length relationship

$$W = \alpha_1 L^{\alpha_2}$$

where L_∞, K, s_0, α_1, and α_2 are constants. The values of these fish growth parameters used in the model, simplified for making theoretic comparisons, are presented (Table 1). We assumed that all fishes that survive through a given time step grow at the growth rate specified by the von Bertalanffy equation above. We assumed that when the food available to the fishes during a particular time step fell below maintenance levels, this translated directly into mortality rather than stunting growth (DeAngelis et al. 1997).

Mature fish produce a number of viable offspring, denoted by "repr" per reproductive bout. We assigned age of maturity, fecundity, and months during the year in which each functional group reproduced based on empirical data. The model embodies three types of mortality assumptions (Table 2). (*i*) Density-independent background mortality, i.e., the natural mortality of an uncrowded population, of each fish size-class. (*ii*) Density-dependent mortality from starvation. This was calculated by first computing the density of resources. As the ratio of total fish biomass to total resource amount increases, the mortality rate applied to fish increases. This mortality is applied equally across species and age-classes. (*iii*) Loss from drying of the cell. When a cell dries, we assumed that some fraction of fish was able to move to an adjacent flooded cell (see Movement section below). The remainder stays in refugia (e.g., alligator ponds) but suffer mortality at a high rate from crowding, oxygen depletion, and predation.

Table 2. The two survival functions used in ODFISH (one-dimensional fish model).

Density-dependent survival	ddsurviv = $1/(1 + F_b/R)$
Size-dependent survival	sdsurviv = $1.0 - F_p/(1 + F_a s)^2$

Note: R is available food (g·m^{-2}·day^{-1}), and s is age (10-day age-classes).

Movement

The environmental driving variable for movement is the water depth (Trexler et al. 2002). When water depth in a cell falls to zero, a fraction of the fish, "disp", moves to an adjacent cell that is still flooded. The rest are subjected to rapid mortality. When a cell refloods, a fraction of fish, assumed here to be the same disp, moves from the adjacent lower elevation cell. Fish move only when their current cell dries out or an adjacent cell refloods.

Simulation runs

Simulations were performed for small Everglades fishes to show the plausibility of the assumed trade-offs for permitting coexistence of species. Three general types of simulations were performed using ODFISH. The first were simulations of a single species with different sets of life history traits to test whether the model projected reasonable spatiotemporal fish density patterns and to determine the effect of each trait on the dynamics of the population. The second type of simulation consisted of two species competing for the same resource to determine the degree of differences in the traits among species necessary for coexistence. The third simulations were of several species competing for the same resource to determine whether the proposed mechanism of

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trade-offs in the two traits permitted multispecies coexistence for reasonable parameter ranges.

Simulations of individual species populations

We assumed that the species within the fish community differed along two trait axes, each being a trait that affected the ability of the fish species to survive in the environment: (*i*) efficiency of resource exploitation, reflected in a different population growth rates (five different reproductive rates), and (*ii*) colonization of reflooded areas (six rates of dispersal).

Our simulations examined the spatiotemporal dynamics of single-species populations for the sets of assumed values of these parameters. We defined a dispersal coefficient, disp, to represent the fraction of fish able to move from one cell to the adjacent flooded cell when the initial cell dried and that were able to move in the other direction to a newly flooded cell. The following values were used: disp = 0.10, 0.15, 0.20, 0.30, 0.40, and 0.50. In all cases, we assumed that female fish attained sexual maturity at 30 days and that a mature female had a reproductive bout every 10 days. The number of successful offspring produced per fish per bout, reflecting resource use efficiency, was set at repr = 4, 5, 6, 7, and 8 (precise estimates of fecundity are difficult to obtain, but these values are consistent with fertility data of Breder and Rosen (1966) and Fuller and Travis (2001)). All possible combinations of disp and repr were studied. Each simulation was run for at least 3650 days (10 years). For each run, we seeded the elevational gradient with an initial population of fish. Several hundred days were allowed for the initial transient dynamics to play out before results were recorded.

Simulations of two competing species

We simulated pairs of species, each drawn from a set of life histories characterized by fecundity and dispersal rates, such that there were trade-offs in these traits. The species with the greater resource use efficiency was slower than the other in dispersing into new areas. The existence of such trade-offs in capabilities is considered an essential factor in explaining the coexistence of species using similar resources (e.g., Roff 1992; Stearns 1992; Rosenzweig 1995). We provided two competing species with different fecundities (repr): Species 1, $repr_1 = 5.4$, and Species 2, $repr_2 = 5.3$. The dispersal rate of Species 1 was $disp_1 = 0.02$, whereas that of Species 2, $disp_2$, was allowed to vary. We performed simulations >50 000 days to determine when coexistence or extinction of one species occurred.

Simulations of a community of competing species

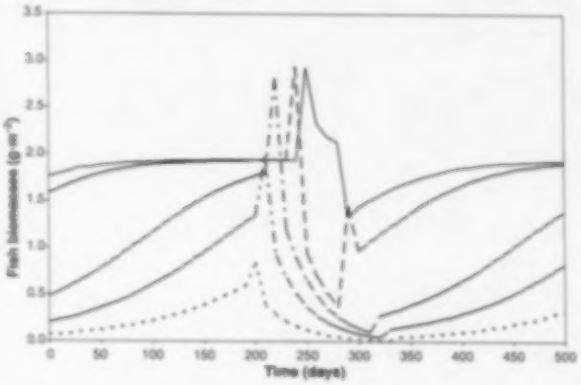
We performed simulations for five different fish species competing simultaneously to see which combinations of life history traits were able to coexist. Strict trade-offs were not assumed in these simulations. As in the two-species case, only the traits of offspring number and dispersal rate were permitted to vary. Simulations were run >50 000 days.

Results

Simulations of individual fish species populations

After several hundred days in a particular simulation, the initial transients died out and the dynamics of the population settled into a regular pattern of seasonal variation. Several features of the seasonal biomass trajectories of fish varied in response to hydroperiod (Fig. 3) First, mean biomass in spatial cells with longer hydroperiods was higher, and fish in cells with the longest hydroperiod may have approached the carrying capacity of those cells. Second, biomass in any given cell rose gradually, ending in a sharp peak, followed by a drop at least as sharp and then a slower, but still rapid decline. This was followed by a brief sharp rise,and then, again, a gradual rise in biomass. The gradual rise occurred after reflooding when the population reestablished. The peak occurred when the cell immediately upstream dried, resulting in an influx of fish dispersing from that cell. When a given cell dried, a sharp decline occurred in the population because of emigration to the adjacent downstream cell. The remaining fish in that cell were assumed to die. After a dry period, the cell flooded again and there was a pulse of immigrants from the adjacent downstream cell. Then the population grew steadily again.

Fig. 3. Illustration of the temporal patterns of biomass of a single species in selected cells over a period of 500 days after all transients have disappeared (solid line, Cell 3; long-dashed line, Cell 4; dot-dashed line, Cell 7; dot-dot-dashed line, Cell 9; short-dashed line, Cell 11; representing longer to shorter hydroperiods). Note the biomass peaks as the cells upstream dry and fish move down-gradient.



Both traits had strong effects on the spatiotemporal population dynamics. To compare the impact of different assumptions of dispersal and fecundity, we plotted the biomasses attained by the late wet season (just prior to immigration influx from the drying upstream cell) in each cell during the year. The results (below) provided profiles of the maximum biomasses attained within the 32 cells along the elevation gradient.

Dispersal rate

We set the fractions of fish able to disperse from drying to wet cells to disp = 0.10, 0.15, 0.20, 0.30, 0.40, and 0.50 (with the other parameter value repr = 6). Below Cell 8, the fish were able to attain close to their carrying capacities for all levels of drydown survival. Above Cell 17, fish could barely attain a fraction of their carrying capacity even for a very high survival rate (Fig. 4). This suggests that there is a lower limit on hydroperiod, below which the buildup of appreciable biomass is difficult. Low dispersal rates did not limit maximum biomass in cells with long hydroperiods, and

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Fig. 4. Profiles of maximum biomass along the elevational gradient for a single species with the dispersal rate disp = 0.10 (shaded line), 0.15 (short-dashed line), 0.20 (dot-dot-dashed line), 0.30 (dot-dashed line), 0.40 (long-dashed line), and 0.50 (solid line). Fecundity is the same in each case, repr = 6.

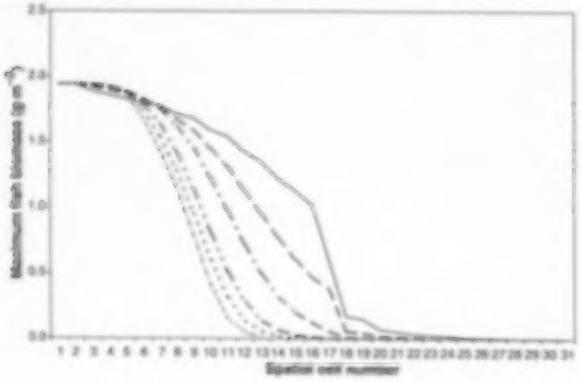
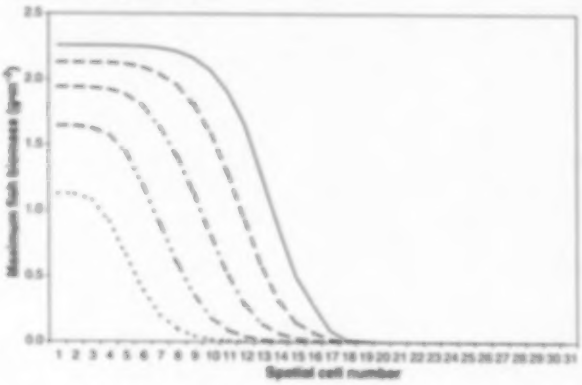


Fig. 5. Profiles of maximum biomass along the elevational gradient for a single species with the fecundity rate, repr = 4 (short-dashed line), 5 (dot-dot-dashed line), 6 (dot-dashed line), 7 (long-dashed line), and 8 (solid line). Dispersal is the same in each case, disp = 0.20.



high dispersal rates did not lead to accumulation of appreciable biomass in the cells with hydroperiods below about 6 months.

Reproduction

For fish reaching maturity at 30 days with reproductive bouts every 10 days, we set numbers of successful offspring produced per bout, repr = 4, 5, 6, 7, and 8 (with the other parameter value disp = 0.20) (Fig. 5). Once again, this range of values had little influence on fish biomass in cells with hydroperiods shorter than about 6 months. However, low numbers of offspring (four or five) affected the accumulation of biomass in all cells because low reproductive rates shifted the steady-state values of fish biomass toward lower levels.

A strong implication of each comparison of spatial profiles of maximum biomass is that cells with hydroperiods less than 6 months are unlikely to build up appreciable fish biomass, even for species with life histories predisposed to increase biomass. An alternative explanation is that short-hydroperiod, high-elevation cells are so far from refuges (continuously flooded cells acting as sources of fish) that they cannot sustain high fish biomass (i.e., they act as population sinks). We tested this alternative hypothesis by making Cell 10 into a permanent waterbody, thereby moving a continuous source of fish closer to the high-elevation cells. The results did not change when the second experiment, that of varying dispersal rates, was repeated. Cells with hydroperiods less than 6 months still failed to accumulate fish biomass, reflecting the lack of time for an invading population to go through more than a few generations. This result could change for species with much higher intrinsic growth rates.

Simulations of two competing species

We provided the two competing species with different fecundities per fish per bout (repr): Species 1, $repr_1$ = 5.4, and Species 2, $repr_2$ = 5.3. Species 1 had dispersal rate $disp_1$ = 0.02, while that of Species 2, $disp_2$, was allowed to vary. Species 2 reached extinction for $disp_2$ = 0.05, 0.08, 0.10, and 0.11. Coexistence occurred for $disp_2$ = 0.12, 0.15, 0.20, and 0.30. Thus, a species with lower fecundity must have a dispersal rate that exceeds some threshold relative to the dispersal rate of the other species to coexist. We also simulated pairs of species with one fish species superior to the other in both fecundity and dispersal ability. The superior species displaced the other in all cases.

Simulations of a community of competing species

We simulated simultaneously five species with various combinations of fecundity and dispersal rate (the choice of five was arbitrary — it may be possible for additional fish species to coexist). In general, coexistence required that differences in repr among the species be proportionally smaller than the differences in the trade-off trait disp, that is, small relative differences in repr have a large effect. Given these conditions, many combinations of values produced coexisting communities. Here, we show the results of one such multispecies assemblage to demonstrate that communities of at least five species can coexist indefinitely in competition for a single resource type, where the resource type is produced independently in spatial cells along an elevation gradient and where fish have both different resource consumption efficiencies and different dispersal rates. The temporal dynamics of biomass of each of the five species populations in a particular cell undergo continual 2-year cycling (see Fig. 6 for a 2000-day period starting at a point 50 years into the simulation).

Population dynamics differed among spatial cells. For example, Species 3 shows 2-year cycles in biomass density in the cells (3, 4, 7, 9, and 11), with the maximum biomass declining along the elevation gradient (Fig. 7 shows an 800-day period). (These cells were chosen arbitrarily for display. The other cells follow similar patterns.) Note that sharp increases occurred when drying of the adjacent upstream cell forced fish to move into a cell. The fish in a particular cell disappeared soon after it dried down, but the cell was recolonized from the adjacent downstream cell when it reflooded.

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Fig. 6. Illustration of the temporal patterns of biomass of five fish species in Cell 3 over a 2000-day period starting 50 years into the simulation. The parameter values for Species 1–5, respectively, are repr = 5.32, 5.33, 5.23, 5.1, and 4.9 and disp = 0.02, 0.25, 0.35, 0.45, and 0.55. Solid line, Species 1; long-dashed line, Species 2; dot-dashed line, Species 3; dot-dot-dashed line, Species 4; short-dashed line, Species 5. Note that the biomass peaks as the cells upstream dry and fish move down-gradient.

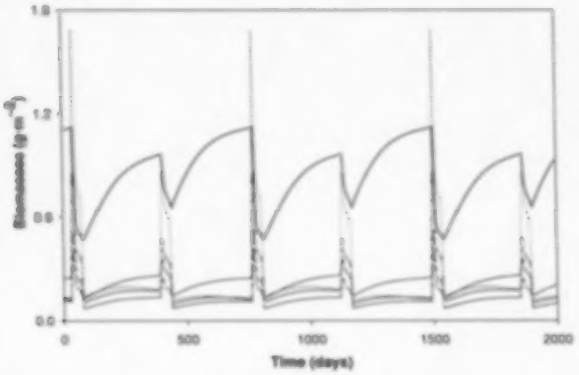
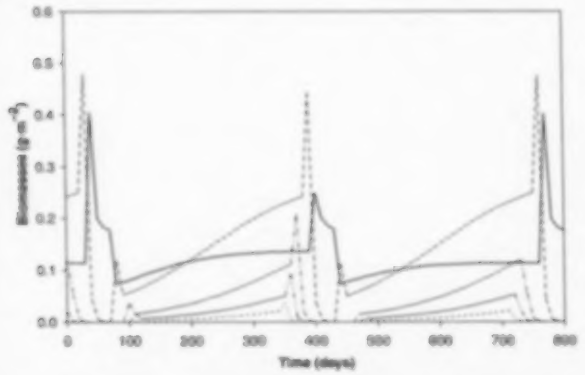
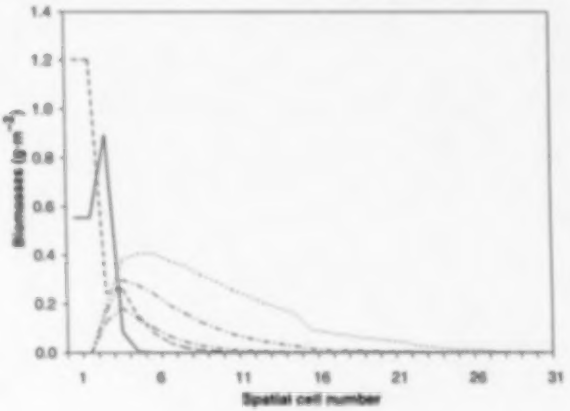


Fig. 7. Dynamics of one of the five species in competitive coexistence (Species 3) in five different cells (3, 4, 7, 9, and 11) over an 800-day period (solid line, Cell 3; long-dashed line, Cell 4; dot-dashed line, Cell 7; dot-dot-dashed line, Cell 9; short-dashed line, Cell 11). Note that sharp increases occurred when drying of the adjacent upstream cell forced fishes to move into the cell. The parameter values for Species 1–5, respectively, are repr = 5.32, 5.33, 5.23, 5.1, and 4.9 and disp = 0.02, 0.25, 0.35, 0.45, and 0.55.



The biomass of all of the species populations along the entire elevation gradient can be compared in the model on any day. It is interesting to compare biomasses of five species late in the wet season, when they build to their highest levels. The distribution of biomass for five species across all cells late in the wet season shows Species 3, 4, and 5 excluded from the two lowest elevation cells and Species 1 and 2 skewed towards those cells (Fig. 8). A noteworthy result in the simulation is that the fish reaching the highest biomass in Cells 1 and 2 (Species 2) had the highest fecundity (by about 2%) and was a better disperser than that with second highest fecundity (Species 1). Nonetheless, Species 1 was able to coexist.

Fig. 8. Biomasses of five coexisting species' populations along the entire elevational gradient on a day late in the wet season. Solid line, Species 1; long-dashed line, Species 2; dot-dashed line, Species 3; dot-dot-dashed line, Species 4; short-dashed line, Species 5. The parameter values for Species 1–5, respectively, are repr = 5.32, 5.33, 5.23, 5.1, and 4.9 and disp = 0.02, 0.25, 0.35, 0.45, and 0.55.



Discussion

Comparisons of data from field studies with models

A primary goal of studies of South Florida fish communities has been to understand their role in transferring biomass to higher trophic levels. These studies are also producing information relevant to the general community theory embodied in the model of southern Florida wetland fishes described here.

All common small-bodied fishes inhabiting the South Florida wetlands have relatively short generation times of only a few months. The South Florida fishes cannot be easily classified into life history categories such as the gleaners and opportunists. Flagfish, marsh killifish (*Fundulus confluentus*), and eastern mosquitofish are closest to matching the characteristics of opportunists, but we know little about the relative contributions of local drydown survival and long-distance migration in explaining their quick recolonization after a drydown. Further, we have only limited information on the competitive hierarchy of these species, although mosquitofish are commonly considered aggressive and superior competitors. There is some evidence that resources are limiting at the densities experienced by mosquitofish in long-hydroperiod habitats and that size-structured interspecific competition takes place (Taylor et al. 2001). The densities observed in short-hydroperiod habitats may be low enough to relax resource limitation. Consistent with this current lack of information on South Florida fishes, we did not try to specifically model the gleaners and opportunists of current ecological theory (e.g., see Litchman and Klausmeier 2001) but merely examined trade-offs in dispersal ability versus greater competitive ability (greater reproductive rate).

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One area in which the results from ODFISH corroborated empirical results was their strong indication that there is a hydroperiod threshold below which fish apparently cannot build up in biomass. Field data demonstrate that densities of fishes are lowest in the short-hydroperiod wetlands and increase with lengthening flooding periods (Trexler et al. 2002). In the model, hydroperiods below about 6 months simply did not provide the opportunity for enough generations of fish to produce a significant population, even when the traits were pushed to high levels within their regions of feasibility. The age structure incorporated in the model is partly responsible for this result, which shows the importance of incorporating this aspect of realism.

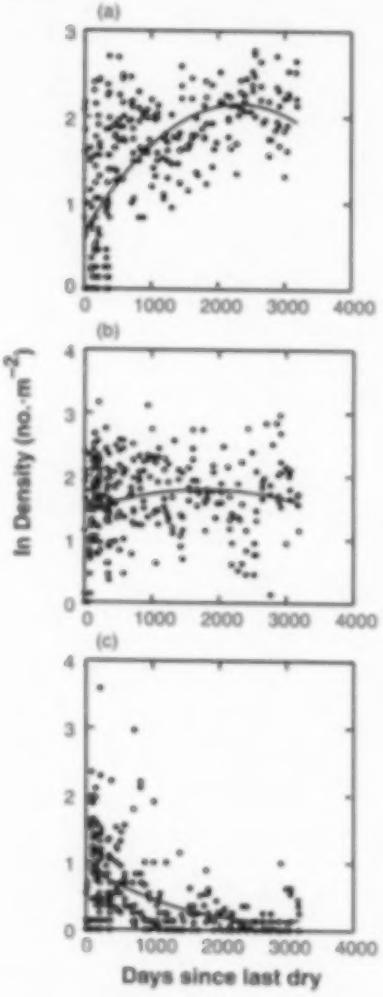
Empirical data also reveal a spectrum of life history traits in fishes (Fig. 9) that support the model projections. For example, following a drydown event at a long-hydroperiod site, three fish species commonly appear soon after the marsh is reflooded. These are the flagfish, marsh killifish, and the eastern mosquitofish. Of these three species, eastern mosquitofish is particularly well known for rapid colonization ability (Brown 1985; Congdon 1994; Baber et al. 2002) and displays no relationship between its density and time since last drydown (Fig. 9). As the time since drydown increases, other species come to dominate the small-fish community, primarily least killifish (*Heterandria formosa*) and bluefin killifish (*Lucania goodei*). The eastern mosquitofish persists at relatively high density as the community is increased with new colonizers. In very short-hydroperiod wetlands, which are subject to intra- and interannual drying, eastern mosquitofish and flagfish colonize the area immediately upon reflooding and dominate the community during the wet season. Although small numbers of other species, such as the killifishes, slowly move into these habitats, they cannot build their numbers before the next drying event.

ODFISH reflects the general features of community expansion into reflooded areas and contraction during the drying period. Some fish disperse more quickly into the newly flooded areas, while others that invade later may come to dominate the community if there is sufficient time. In addition, temporal biomass peaks of the type shown in this study are evident in field data. The detailed spatiotemporal patterns of occupation by the small-fish community and the relationships of these patterns to life history parameters are just beginning to be studied, however, and cannot yet be used to test ODFISH in detail. The model results will serve to guide future observations.

Implications and limits of model

The results of the ODFISH model confirmed that the general traits of high reproduction and dispersal are important for fishes to persist in the widely varying environments found in southern Florida wetlands. To survive under the conditions imposed by the model, fish species needed high reproduction rates (this does not imply that only highly fecund species will survive in South Florida; our model did not include permanent waterbodies that could support large fishes with competitive advantages other than simply high reproduction). The ability to disperse rapidly enabled fishes with lower reproductive rates to take advantage of newly reflooded areas, where competition for the food supply was low.

Fig. 9. Illustration of three patterns of recovery following drying events by fishes inhabiting a long-hydroperiod site in the Everglades. log-transformed density is plotted against days since the study site last dried. (*a*) Bluefin killifish (*Lucania goodei*); (*b*) eastern mosquitofish (*Gambusbia holbrooki*); (*c*) flagfish (*Jordanella floridae*).



It is difficult to compare these two traits precisely with those in the theoretical literature. Both high fecundity and rapid dispersal are generally considered to be opportunistic traits and so do not form a gleaner–opportunist trade-off axis. Instead, these might be thought of as two types of opportunistic species. In any case, the simulation model corroborated the results of the simple analytic model that trade-offs in these traits can lead to coexistence.

In general, our model is consistent with results of other types of nonequilibrium models of coexistence discussed earlier. But it was unexpected to find in some five-species simulations that a species with lower values of both traits than another species could persist. This seemed to contradict our two-species simulations, which always showed that when one species had both lower resource use efficiency and

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lower dispersal rate than another, it was always excluded. We confirmed that if Species 3, 4, and 5 were removed from the five-species simulation, Species 1 went to extinction. We also extended the simulation time to demonstrate rigorously that the five-species coexistence shown here is real. One possible explanation for the persistence of Species 1 in the five-species case is that the competition of Species 3, 4, and 5 affected Species 2 more strongly than Species 1, as there is more spatial overlap between Species 1 and these other species than between Species 2 and the latter. Although we have not seen this sort of result in the literature on species coexistence in fluctuating environments, it may not be too surprising. Nonlinear, multispecies systems have complex competitive feedbacks that may offset slight inequalities in life cycle fitness in some cases. Thus, the conditions of this model seem to permit exceptions to the general notion that trade-offs in life history traits are required for coexistence (e.g., Roff 1992; Stearns 1992; Rosenzweig 1995). It is interesting to note that empirical data seem to indicate that one Everglades species, the eastern mosquitofish, may be superior to many other species in both of these traits, which does not affect the coexistence of those species in the ecosystem.

Like all models, ODFISH is a compromise between the inclusion of enough mechanistic detail that we believe is important and the simplicity that is essential in interpreting the results. It is useful to briefly review the main simplifications of the model that could affect results. (*i*) Space is modeled as one-dimensional with a linear gradient (divided into 250-m cells). (*ii*) The seasonal fluctuations are sinusoidal with no interannual variations. (*iii*) All fish species followed the same von Bertalanffy growth pattern and had identical energetics and ages of first reproduction. They differed only in the two traits studied. (*iv*) There are implicit assumptions in the model concerning how fast fish move from one spatial cell to the next. (*v*) We did not include refugia (e.g., alligator ponds) within cells, which could allow some fish to survive in a cell after water depth dropped below zero in the cell. (*vi*) Predators on the fishes were not considered. They may be an important limitation on fish densities in the long-hydroperiod marshes.

These simplifications are necessary for the model to be useful in exploring theoretical questions. However, they limit the applicability of the model to studying management issues in detail. What the model does show is that a wide spectrum of hydroperiods is probably one of the underlying reasons for the diversity of the fish community in the Everglades wetland. The model also reinforces empirical indications that areas with hydroperiods of less than about 6 months do not produce large amounts of fish biomass. To answer the highly specific management questions required for South Florida restoration, larger models (e.g., Gaff et al. 2000), which can utilize detailed hydrology models of the landscape of southern Florida, must be used.

ODFISH can, nevertheless, be extended in the future to provide some general answers to certain critical questions. For example, how do large piscivorous fishes, which may move into the wetlands when water depths are deep enough, affect the small-fish community? How does the presence of large aquatic refuges like canals or river channels affect the large fish – small fish dynamic, and how far into the wetlands is the effect felt? Are there particular life history characteristics that render a potential invasive species especially onerous? These features can be addressed in the present model. A lingering question for managers is how high densities of fishes develop and are made available to predators in the wetlands. In the past, large colonies of wading birds occurred in certain years at certain places in the Everglades, presumably owing to high concentrations of fish prey (Frederick and Ogden 2001). Those concentrations were likely related to aspects of hydrology, such as water recession rate and local pooling of water based on topography. Recession rate affects shorter term processes like fish mortality through stranding or in refuges and their availability to predators. But other processes, including plant and animal succession, predator–prey relationships, and nutrient processes, all of which depend on hydroperiod, may also be involved. Extensions of the model may be needed in these directions.

ODFISH has revealed other questions that need to be addressed empirically. These include how fast fishes can follow the wetted front. Are their movement rates the same both under recession and flooding? What are the rates of fish survival in local refuges during drydown, and do those fishes play a significant role in colonizing reflooded areas? What features should invaders have to successfully become established in the community? These and other questions will guide collaborative field and modeling research in the future.

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Can commercial fishing cause evolution? Answers from guppies (*Poecilia reticulata*)[1]

David N. Reznick and Cameron K. Ghalambor

Abstract: Life history theory predicts that high adult mortality rates select for earlier maturity and increased reproduction. If such evolution occurs in response to the commercial exploitation of natural fish populations, then the correlated reduction in body size would reduce the yield of the fishery. Earlier maturity and reduced body size are seen in commercially exploited populations. Here, we compare the life histories of natural populations of guppies (*Poecilia reticulata*) from Trinidad that live in either high- or low-predation environments, which serve as surrogates for the presence or absence of commercial fishing. We can quantify mortality rate and life history variables, including age and size at maturity, in the laboratory and in nature. We have manipulated mortality rates in nature and measured the rate of evolution. High mortality selects for earlier maturity at a smaller size, as observed in commercial fisheries and as predicted by theory. Furthermore, the nature and magnitude of predator-induced mortality are comparable to those caused by commercial fishing. The rate of evolution in guppies predicts similar evolution in commercial fisheries on a time scale of decades. These attributes support arguments that humans, like predators, have acted as an agent of selection when exploiting populations of fish.

Résumé : La théorie démographique prédit qu'une forte mortalité des adultes entraîne la sélection d'une maturité précoce et d'une reproduction accrue. Si une telle sélection se produisait en réaction à l'exploitation commerciale des populations naturelles de poissons, la réduction de la taille corporelle, un effet en corrélation, réduirait le rendement de la pêche. La maturation précoce et la taille réduite s'observent dans les populations exploitées commercialement. Nous comparons ici les cycles biologiques de populations naturelles de guppys (*Poecilia reticulata*) de Trinidad qui vivent dans des milieux de forte ou de faible prédation, ce qui sert ici de phénomène de remplacement pour la présence ou l'absence de pêche commerciale. Nous pouvons mesurer le taux de mortalité et les variables démographiques, en particulier l'âge et la taille à la maturité, en laboratoire et en nature. Nous avons manipulé les taux de mortalité en nature et mesuré le taux d'évolution. Une forte mortalité entraîne la sélection d'une maturité à une taille réduite comme on l'observe dans les pêches commerciales, en accord avec la théorie. De plus, la nature et l'importance de la mortalité induite par les prédateurs sont comparables à celles causées par la pêche commerciale. Le taux d'évolution observé chez les guppys permet de prédire une évolution semblable dans les pêches commerciales sur une échelle de décennies. Ces caractéristiques appuient les arguments qui veulent que les humains, tout comme les prédateurs, aient agi comme agents de sélection naturelle en exploitant les populations de poissons.

[Traduit par la Rédaction]

Introduction

The principles of stock management are based on population dynamics. The goal is to evaluate how many individuals within a population can be harvested without overharvesting and reducing future yield. An implicit assumption of such formulations is that the population does not evolve and that management can be based solely on inferences derived from the direct assessment of the target organism (Hilborn 2003). The theory of life history evolution, which was developed independently of any applied goals, addresses the same phenomenon as the principle of sustainable yield, which is to evaluate the consequences of extrinsic mortality, or mortality imposed from outside the organism such as by disease or predation (Roff 1992; Stearns 1992). The goal of life history theory is to consider how such mortality can influence the evolution of traits that determine how organisms allocate resources to reproduction. These traits include variables such as growth rate, the age and size at maturation, and the proportion of available resources that are devoted to gamete production as opposed to growth and maintenance.

The management of exploited, natural fish populations and the study of life history evolution share the common theme of evaluating the consequences of externally imposed

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D.N. Reznick.[2] Department of Biology, University of California, Riverside, CA 92521, USA.
C.K. Ghalambor. Department of Biology, Colorado State University, Fort Collins, CO 80523, USA.

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[2]Corresponding author (e-mail: david.reznick@ucr.edu).

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mortality, be it by fishing nets, predators, or disease. The possible connection between life history evolution and the exploitation of natural resources was suggested by Ricker (1980) but did not begin to be formalized until the late 1980s (Law and Grey 1989). The reasons for making this connection are more than academic. The problems with commercial fisheries are not simply that stocks are being depleted. Exploited fish stocks are changing. Body sizes and growth rates are declining (Ricker 1980; Rijnsdorp 1993). Populations are failing to rebound or are rebounding very slowly after fishing pressure is reduced (Hutchings 2001). The composition of natural communities is changing (Greenstreet and Hall 1996; Jennings and Kaiser 1998; Jennings et al. 1999). Among all of these unexpected changes, it is relevant to consider that the mortality induced by harvesting may be serving as an agent of selection and that the exploited fish stocks have evolved.

Conceptualizing commercial fishing as an agent of selection that causes target species to evolve demands that we change the popular concept of what evolution is like. The common perspective of evolution, as originally conceived by Darwin (1859), is that of a very slow, gradual process that is not discernable within the lifetime of an investigator but can have profound effects over large time scales. The consequence of this perspective is that people tend to think of ecology and evolution as being clearly separable, as in the case of fisheries stock assessment versus life history evolution, or that evolution need not be considered an integral component in the study of ecological processes. Recent work, all postdating 1980, demonstrates emphatically that this is not true. Under the appropriate circumstances, organisms readily evolve quickly enough for such changes to affect short-term ecological interactions (Thompson 1998; Hendry and Kinnison 2001).

Guppies (*Poecilia reticulata*) as a model system

Here, we present a synopsis of ongoing studies of natural populations of guppies that have enabled us to evaluate the effects of mortality on the evolution of life histories, the rate at which organisms can evolve, and the potential role of indirect effects of predation or the way predation interacts with other aspects of the ecology of guppies. In guppies, mortality is caused by predation, so we are equating predation with the mortality induced by fishing. The virtue of this study system is that it is possible to study comparative ecology, population biology, and evolution with far more precision than would be possible in commercially exploited species of fish. If we accept that the underlying principles of ecology and evolution can be generalized, then it is arguable that this system can serve as an experimental model that can help us to understand the workings of less manageable species and communities.

Advantages of working on guppies include their short generation time, small body size, and amenability to laboratory and field studies. Male guppies attain maturity in as few as 6 weeks and females give birth to their first litter of young when as young as 9 weeks (Reznick 1982; Reznick and Bryga 1996). An adult male is around 15 mm long and an adult female ranges from 18 to 35 mm, so they are easily housed in small aquaria without highly specialized filtering systems. They are livebearers, so the young are like miniature adults that thrive on the same care as the adults. The probability of survival from birth to maturity is exceedingly high, so it is easy to make comparisons among populations in the laboratory without inadvertently introducing biases into the comparisons, such as selecting for laboratory-adapted lineages. Such nonselective propagation is ensured by rearing all young and then randomly selecting an equal number of young for representation in the next generation and crossing them in a breeding design that equally represents the original population sample (Reznick 1982). A consequence of their tropical origins is that they readily breed throughout the year in the laboratory without the requirement of any environmental cues.

The guppy populations that we study are from the Northern Range Mountains of the island of Trinidad. An inherent property of these small mountain streams and being on an island is that the natural communities are simple in comparison with what you might find elsewhere in the tropics. We have focused on the comparison between high versus low mortality rate environments. Mortality rate is determined by the predators that co-occur with guppies. In high mortality rate environments on the south slope of the Northern Range, guppies co-occur with predators like the pike cichlid *Crenicichla alta*, characins like *Astyanax bimaculata* or *Hemibrycon dentatum*, or the wolf fish *Hoplias malabaricus*. These species are a subset of what would be found in freshwater streams of mainland South America. On the north slope, the key predators are instead species derived from a marine environment, including gobies (*Eleotris pisonis*, *Gobiomorus dormitor*, and *Dormitator maculatus*) and mullets (*Agonostomus monticola*). Low mortality rate environments are found in the same streams as high-predation environments but upstream of barriers that exclude the upstream migration of the predators. Here, guppies generally co-occur with just the killifish *Rivulus hartii* on the south slope and *Rivulus* plus prawns in the genus *Macrobrachium* on the north slope. An important feature of this setting is the difference in the composition of the high-predation communities on the two slopes. If mortality is what counts in shaping life history evolution, then it should not matter who the predators are but what the mortality rate is. A second important feature of this setting is that this contrast between high and low predation is repeated in several drainages, which yields multiple replicates for making the comparison between high- and low-predation environments. In some cases, there is sufficient genetic information available to also argue that a given drainage represents an independent replicate in which guppies have adapted to either high or low predation (Carvalho et al. 1991; Fajen and Breden 1992). For example, the guppies from the Oropuche drainage are genetically very distinct from those in the other drainages, regardless of whether they are from high or low mortality rate environments. They display the same life history differences between high- and low-predation environments as seen in other drainages, so it appears that guppies from the Oropuche drainage have adapted to these different environments independently of those elsewhere on the island.

The physical structure of these streams also facilitates population studies. Many of the streams where guppies are

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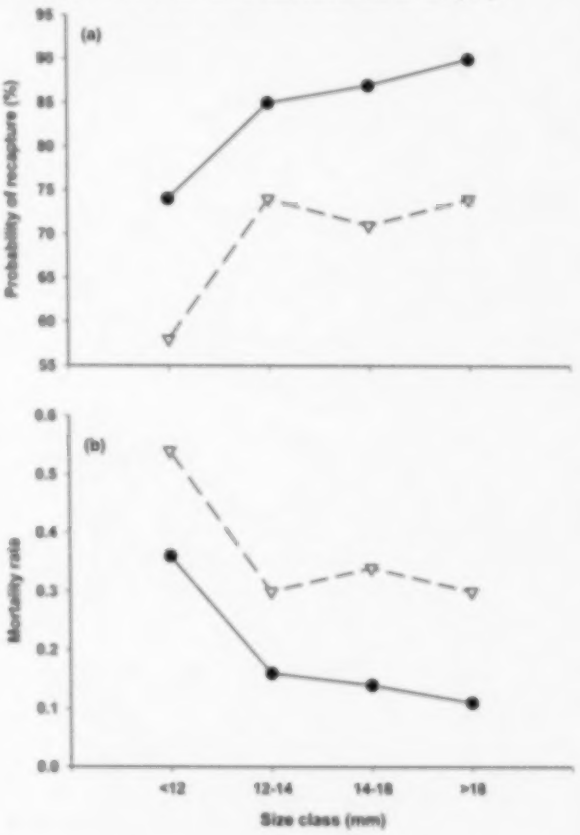
found are small and have a pool–riffle structure. By small, we mean that the widths are often one to a few metres and average depths are a few tenths of a metre. These streams are divided into pools that have relatively low flow rates and are separated from one another by discrete riffles where the water flow rate is higher. Guppies tend to aggregate in pools and have restricted movement from one pool to another. It is possible to catch nearly all of the fish in a pool in a limited amount of time, to then mark and measure and release them for later recapture. In our most recent large-scale mark–recapture studies, we estimated that the probability of recapturing a given fish on a single visit, if it was still alive, was 96.7% and 91.7% in two replicates (Bryant and Reznick 2004). These studies involved dozens of pools and thousands of fish. Our recapture probabilities are higher in smaller scale studies such as those summarized in Fig. 1 (from Reznick et al. 1996*a*). In such a setting, it has been possible to characterize the differences in mortality rates that the guppies experience in high versus low mortality rate environments. We have used these methods to compare the mortality rates of guppies from high- and low-predation environments and show that there are substantially and significantly higher mortality rates in high-predation environments (Reznick et al. 1996*a*).

Fig. 1. (*a*) Modified from Fig. 2*b* in Reznick et al. (1996*a*). Recapture probabilities of marked fish from 14 mark–recapture assays done in seven high- and seven low-predation localities. The probability of recapture is a very good estimate of the probability of survival, so 1 minus these estimates equals the probability of mortality. The time interval was 12 days. These data show that the recapture probability of guppies (*Poecilia reticulata*) in high-predation sites (triangles) is significantly lower than those from low-predation sites (circles) or that they have a significantly higher mortality rate. The <12 and 12–14 mm categories are immature fish. The 14–18 mm size-class includes all mature males and females that are producing their first or second litter of young. The >18 mm size-class is exclusively mature females that are producing their second or subsequent litters. Note that the results for the largest size-class imply that guppies from the higher predation site suffer a nearly threefold higher mortality rate. (*b*) Absolute mortality rate (larger numbers represent higher mortality) based on the same data calculated as $\ln(N_t/N_0)$.



Guppy life histories

We have evaluated the life histories of guppies from high- and low-predation environments in two ways. First, we quantify different aspects of the phenotypes of wild-caught fish, including the size distribution of reproducing individuals, fecundity, offspring size, and the proportion of body weight that consists of developing embryos, which we call reproductive allocation. Second, we quantify the life histories in the laboratory on the second generation of laboratory-born fish. In this context, we quantify the age and size at maturity, fecundity for the first three litters, offspring size, and other aspects of the life history. The first methodology allows us to sample many localities over a large geographical area but is limited in its ability to quantify traits of interest. The second methodology is far more labor intensive and limits the number of populations that we can sample but affords a much more detailed description of the life history.

Comparisons of wild-caught guppies reveal that those from the high-predation localities are smaller at maturity and produce more and smaller offspring. They also have higher reproductive allocations, or devote a larger percentage of their body weight to developing offspring (Reznick and Endler 1982; Reznick et al. 1996*b*). Figure 2 represents mean values from five high- and eight low-predation sites on the north slope and seven high- and five low-predation sites on the south slope. The high-predation guppies from either slope produce between two and three times as many offspring as equal-sized low-predation females from either slope (Fig. 2*a*). The individual offspring from high-predation localities average around 60% of the dry mass of the offspring produced by females from low-predation localities (Fig. 2*b*). The number and size of offspring can be combined into a single variable called reproductive allotment that represents the proportion of a female's dry mass that consists of developing young. This variable shows that guppies from high-predation localities devote 40%–50% more resources to each litter (Fig. 2*d*). Finally, this figure shows that male guppies from high-predation localities are smaller on average than those from low-predation localities (Fig. 2*c*). Male guppies stop growing when they attain maturity, so the smaller size of males from high-predation sites suggests earlier maturity. We also found that female guppies from high-predation sites give birth to their first litter of young at a smaller size than those from low-predation sites, again suggesting earlier maturity. The nature of the differences in guppy life histories

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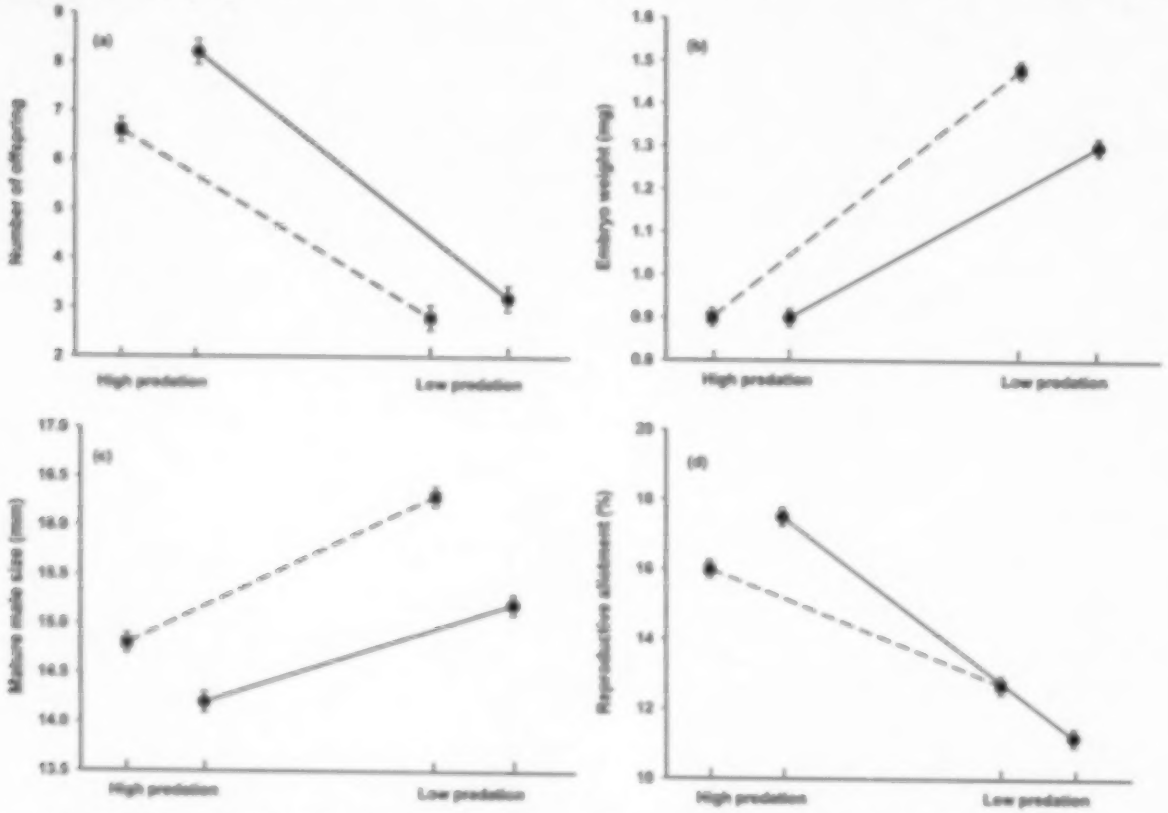
Fig. 2. Modified from Fig. 2 in Reznick et al. (1996*b*). Least squares means (±1 SE) of life history traits from high- and low-predation sites on the north slope (solid line) and south slope (broken line) of the Northern Range Mountains. (*a*) Number of developing offspring per female adjusted for the females' somatic dry weight; (*b*) dry weight of developing offspring adjusted for their stage of development; (*c*) average size of mature males; (*d*) reproductive allotment of females with developing offspring adjusted for the stage of development of the offspring.



between high- and low-predation sites is very similar on the north and south slopes, in spite of the differences in the composition of the predator communities.

In some cases, it has been possible to compare life histories on an even finer geographical scale (Fig. 3). For example, the Aripo River contains a barrier waterfall that excludes predators but not guppies, so it is possible to compare the life histories of populations that are found only tens of metres apart, above and below the barrier, in environments that are essentially identical save for the presence or absence of predators. These comparisons show that the differences in life history phenotype can be seen in populations that are found in the same stream where the only clear difference between the localities is the presence or absence of predators. In this case, there were four samples collected from low-predation sites above the barrier waterfall, all of which have very similar life histories that are typical of low-predation localities. There is a fifth sample that was collected approximately 600 m below the barrier waterfall that has a life history that is typical of a high-predation locality. The sample collected from the high-predation site immediately below the barrier differs significantly from that collected immediately above it, and the differences are consistent with those that usually characterize high- and low-predation environments, but the values immediately below the barrier are intermediate to those seen above the barrier and those seen farther downstream. These intermediate values may represent the effects of gene flow or the migration of guppies adapted to low-predation localities above the barrier waterfall into the high-predation site below the barrier waterfall. Such gene flow would cause a mixing of low-predation genotypes from above the barrier waterfall with high-predation genotypes below the barrier waterfall. The disappearance of this effect further downstream suggests that predators have selected against further spread of the low-predation genotypes. Endler (1978) obtained similar results for the color patterns of males found above and below these same barrier waterfalls (see fig. 13 in Endler 1978). These patterns make a compelling case for predators as the cause of these life history differences as opposed to some unrelated environmental factor that is correlated with predators.

Our laboratory assays of the life histories of the grandchildren of wild-caught fish show that the differences persist after two generations in the laboratory experiment that used randomized block arrays for rearing the wild-caught females and both laboratory generations (Reznick 1982; Reznick and Bryga 1996). These studies also include dependent variables that are more relevant to life history theory. Specifically, it is

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Fig. 3. The data for this figure were derived from Table 2 of Reznick and Endler (1982). Each sampling point along the river is represented by the number of offspring per litter, correcting for female body size, and the average dry mass of the offspring (mg), correcting for their stage of development. Offspring tend to lose mass during development. The position of three barrier waterfalls is indicated, as are the different types of predator communities. High predation is represented by a solid line. *Rivulus*-only localities (Low B) are represented by the broken shaded lines. Low A (shaded lines) refers to sites that lack all potential predators found below the barrier waterfall except the cichlid *Aequidens pulcher*. The segments of stream labeled as Downstream control, Introduction site, and Upstream control represent the treatments associated with the predator introduction experiment.

possible to quantify the age at maturity in males, the age at first reproduction in females, and reproductive effort, or the percentage of consumed resources that are devoted to the production of young. The latter variable is estimable because females are reared in isolation and get quantified amounts of food, because we are able to evaluate the resources allocated to each litter of young plus quantify how often the fish reproduce. Guppies from high-predation environments not only devote more resources to each litter but also have shorter time intervals between successive litters, which enhances the differences between the high- and low-predation fish in reproductive effort. Sample results (Fig. 4) show that females from high-predation environments are younger (Fig. 4*a*) and smaller (Fig. 4*b*) when they first give birth than their counterparts from low-predation environments. Likewise, males from the high-predation localities are younger (Fig. 4*c*) and smaller (Fig. 4*d*) at maturity than those from low-predation localities, even when reared in a common environment for two generations. These same studies also reveal that females from high-predation environments give birth to smaller offspring and more offspring per litter and devote a larger percentage of their consumed resources to reproduction, as opposed to growth or maintenance (also see Fig. 2). The same patterns are obtained from fish from the north and south slopes. This methodology thus demonstrates that the differences in life histories can be obtained repeatedly in an artificial environment. Because these estimates were derived from fish reared in a "common garden" setting for two generations, they can be interpreted as representing genetic differences. The differences in individual traits, like fecundity or age at maturity, may seem rather small; however, it is important to realize that there is an internal consistency in the way individual traits differ and that their cumulative effects are much larger than each by itself. Specifically, guppies from high-predation environments have life histories that will result in the more rapid production of young because they begin to reproduce at an earlier age, produce litters more frequently, and give birth to more young per litter.

Experimental evolution

Another outstanding virtue of working on life history evolution in these fish is that it is possible to manipulate the distribution of guppies and guppy predators in natural streams and hence to manipulate guppy mortality rates. Such experiments make it possible to test evolutionary theory in a natural setting plus quantify the rate of evolution.

These experiments are facilitated by the structure of the habitat. Endler (1980), who evaluated the combined effects of predation and sexual selection on the evolution of male coloration in guppies, used the presence of barrier waterfalls to manipulate exposure to predation. He worked in a tributary to the Aripo River that was separated from the main river by a dramatic waterfall. Downstream from the waterfall, guppies were found in a high-predation community. Only *R. hartii* was found above the waterfall. The waterfall thus served as an upstream barrier to the distribution of all fish except *Rivulus*. He collected guppies from the high-predation site below the barrier and introduced them into the low-predation, previously guppy-free site above the barrier. Such a manipulation created an experimental treatment in which guppies experienced a reduction in mortality rate, analogous to the cessation of commercial fishing. We confirmed this reduction in mortality rate with mark–recapture studies (Reznick et al. 1996*a*). This manipulation also had a built in control, which was the high-predation site that they were derived from. The second generation of laboratory-reared offspring from the introduction site and high-predation control can be compared in a laboratory assay to evaluate the ways in which the introduced population has adapted to its new setting. We have also repeated this sort of introduction in a different drainage. The results of these experiments revealed significant increases in the age and size at maturity of males after only 4 years (Reznick and Bryga 1987), in females after 7.5 years (Reznick et al. 1990), and in offspring size, fecundity, and early life reproductive effort after 11 years (Reznick et al. 1990) (Table 1).

We have also performed a different type of introduction that evaluates the effects of increased mortality rate, which is analogous to introducing commercial fishing. In this case, we worked with a barrier on the mainstream of the Aripo that excluded pike cichlids and characins, but not guppies, from the upstream environment (see Fig. 3). There were additional waterfalls upstream that were as dramatic as the one that excluded the predators. Here, we introduced pike cichlids over the barrier waterfall. They successfully colonized the habitat and extended their range to the next barrier

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Fig. 4. Modified from Fig. 1 in Reznick and Bryga (1996). Least squares means (±1 SE) for the age and size at maturity in males and the size at first parturition in females from high- versus low-predation environments. (*a*) Female age at first parturition; (*b*) female size (wet weight) just after giving birth to the first litter of young; (*c*) male age at maturity; (*d*) male size (wet weight) at maturity. The fish from the north slope (solid line) were evaluated at a different time from those on the south slope (broken line) and were reared on lower levels of food availability. As a result, they tended to mature at an earlier age and smaller size. To facilitate comparisons between the two slopes, we scaled the *y* axes differently so that the proportional differences between high- and low-predation fish from each slope were the same.

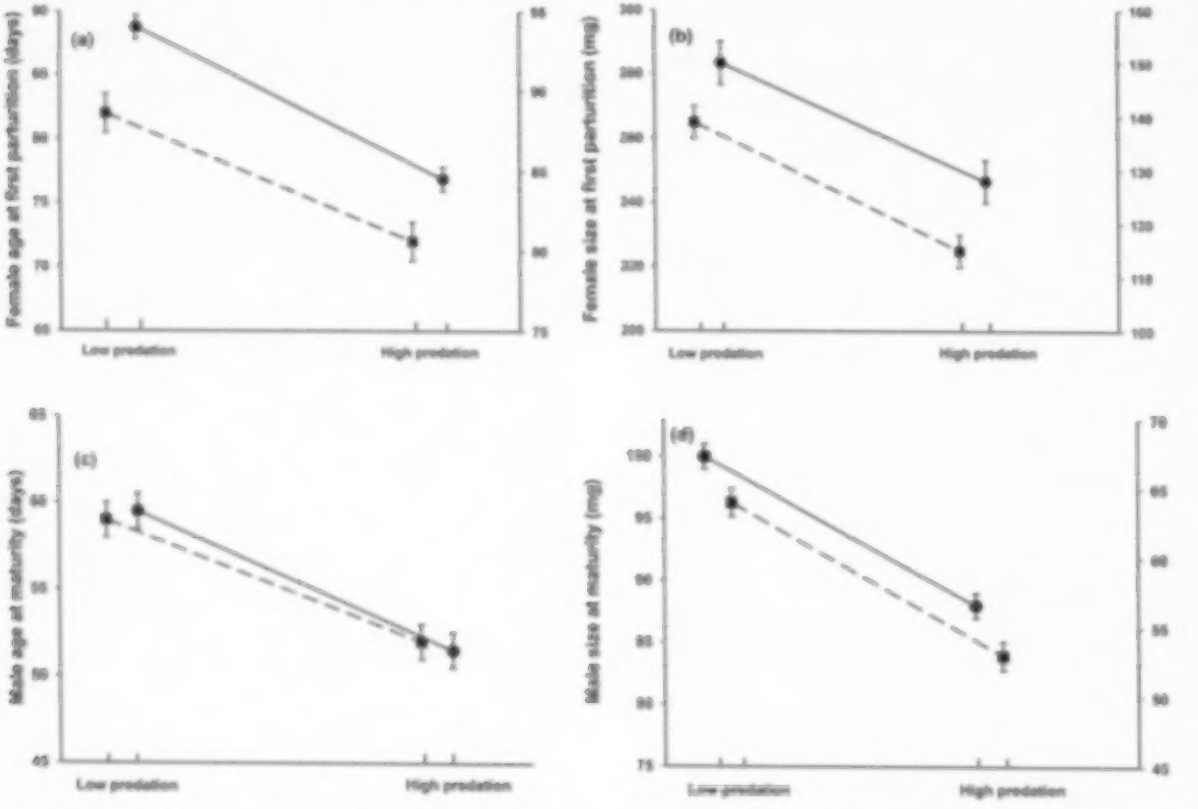

Table 1. Summary of the ages and sizes at maturity in the predator introduction experiment on the Aripo River.

	Downstream (high)	Introduction (low to high)	Upstream (low)
Male age (days)	48.4	52.4	56.3
Male size (mg)	67.5	76.6	80.2
Female age (days)	85.1	91.0	95.0
Female size (mg)	160.4	184.4	192.8

Note: Horizontal lines join means that do not differ significantly from one another.

waterfall upstream. This manipulation created an experimental population that experienced increased mortality rates and was bounded by a low mortality rate control upstream and a high mortality rate control downstream. Adding predators resulted in the evolution of the same differences in life histories between the experimental and control populations as seen when comparing low- and high-predation populations. Specifically, after only 5 years, the experimental populations were intermediate between the high- and low-predation controls in the age at maturity in males and the age at first parturition in females (Reznick 1997). Since an assay performed before the predator introduction showed that these fish were equal to the low-predation control, the results 5 years after the introduction show that the introduction of predators had selected for earlier maturity.

These experiments reveal some important details that cannot be obtained from the earlier comparative studies. First, they greatly strengthen the argument that predation and predator-induced mortality play a significant role in shaping the evolution of life history traits through direct experimentation. Second, they show that evolution can happen very quickly and on a time scale that is observable within the lifetime of the investigator. Even though these changes in body size and life history traits seem subtle, if we were to evaluate the rate of change on the same time scale as we judge the fossil record, then we would find that it is four to seven orders of magnitude faster (Reznick et al. 1997). These large

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differences in the estimated rate of evolution from contemporary studies versus the fossil record are likely attributable to rates from the fossil record being systematically biased because it averages changes in the direction of evolution and intervals of no evolution. The consequence is that it underestimates the potential rate of evolution (Gingerich 1983; Reznick et al. 1997). The importance of the comparison between the fossil record and contemporary studies is that the fossil record has generally shaped our impressions of what the process of evolution is like and is the source of the assumption that evolution is a slow process that would not be observable in brief intervals of time (Reznick and Ghalambor 2001).

Indirect effects

The body of theory that has been developed to describe life history evolution in commercially exploited fish populations argues that the indirect effects of fishing-induced mortality may be as important in shaping life history evolution as direct effects. Direct effects refers to the increase in mortality rate caused by harvesting. Indirect effects refers to all of the ways in which harvesting can interact with other types of ecological processes. Harvesting will reduce the density of the target species, which may result in higher food availability for the survivors, but may also alter ecological interactions between the target species and other elements of the community in which it is found. The potential importance of indirect effects has been explored from a theoretical perspective (Abrams and Rowe 1996; Gardmark et al. 2003; Matsuda and Abrams 2004). All of these papers show that the evolutionary consequences of added mortality caused by fishing or a new predator depend on the ecological context. For example, if the exploited species is a predator and increased mortality results in an increase in prey abundance for the survivors, then the exploited species may not evolve earlier maturity at a smaller size as predicted if the model just includes a predator (fishing) and prey. It is possible to evaluate the potential for indirect effects of predation in our work on guppies.

We have characterized several aspects of the ecology of representative high- and low-predation environments (Grether et al. 2001; Reznick et al. 2001*b*). Some of the differences that we found are attributable to environmental factors that are correlated with predation. For example, low-predation streams are smaller on average than high-predation streams. A direct consequence of their smaller size is that they are narrower and have a more closed tree canopy, lower light levels, and lower levels of primary productivity. The low-predation streams also have a different population structure. There are more large guppies and fewer small guppies than seen in high-predation streams. This difference is best understood as a consequence of the lower mortality rates and lower birth rates of guppies in low-predation environments or as a combined effect of the evolution of their life histories and their lower day-to-day mortality rates (Rodd and Reznick 1997). Fewer young are produced and more of them attain advanced ages. Conversely, more offspring are produced and fewer survive to adulthood in high-predation environments, so there are more small, young fish in these populations. These differences in population structure translate into a fourfold higher biomass per unit area of stream in low-predation sites than in high-predation sites. Finally, we find that, in nature, the guppies from low-predation sites tend to grow more slowly and attain smaller asymptotic body sizes than guppies from high-predation sites (Reznick et al. 2001*b*) but that these differences are not seen when they are reared in a common environment (Reznick and Bryga 1996). In the laboratory, we instead see that increased food causes higher growth rates and larger asymptotic body sizes (Reznick and Bryga 1996), so we infer that the lower growth rates and smaller asymptotic body sizes in low-predation localities are caused by lower levels of food availability in nature.

The differences in density, growth rate, and asymptotic body size can be viewed as an indirect consequence of predation, at least in part. While we have not fully characterized such indirect responses and have yet to critically evaluate their evolutionary significance, it is at least worth noting that they can be evaluated in this system, incorporated into a more complete analysis of adaptation, and hence make it compatible with some of the more recent theory that has been developed to characterize life history evolution in a more complex ecological setting. One obvious consequence of the indirect effect of predation on population density is that guppies from high-predation environments experience higher levels of resource availability than those from low-predation environments. Higher food availability results in earlier maturity at a larger body size (Reznick 1982, 1990). In a fisheries context, the reduced density associated with harvesting can cause an increase in growth rate, particularly in the younger age-classes (Rijnsdorp 1991). What the work on guppies shows is that this environmental effect (i.e., greater food availability) will partially mask how fish life histories will evolve in response to exploitation, since selection favors earlier maturity at a smaller body size, while the increased availability of food causes higher growth rates and larger sizes at maturity. Thus, understanding how both the direct and indirect effects of predation shape the population biology reveals interactions unappreciated by each approach on its own.

What can guppies teach us about the management of natural populations of fish?

Mertz and Myers (1998) proposed a simplified formulation for quantifying the effects of fishing-induced mortality on exploited populations. We have reinterpreted our mark–recapture data (Reznick et al. 1996*a*) in a similar fashion so that we can compare the magnitude of added mortality caused by predators on guppies with that caused by fishing on exploited fish populations. We treat low-predation sites as equivalent to an unexploited fish population so that the instantaneous mortality rates represent natural mortality (M). The high-predation sites are treated as equivalent to an exploited fish population, since they bear the additional mortality caused by predators. Their total mortality consists of natural mortality and the added mortality due to predators (F) and equals the sum of the two ($F + M$). The difference between mortality rates in high- and low-predation localities thus represents the increment in mortality caused by predation (F), which is then scaled by the total mortality rate for

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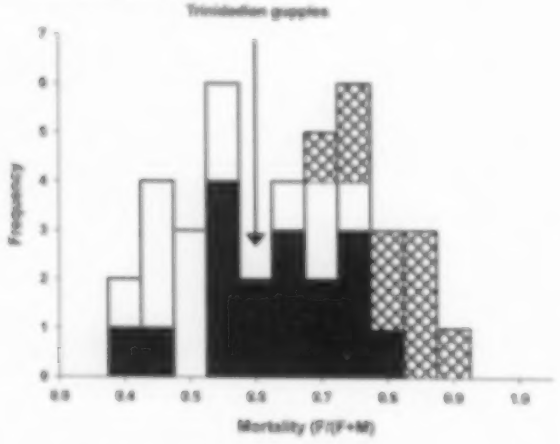
Table 2. A reinterpretation of the mark–recapture data from Reznick et al. (1996*a*) in a fashion similar to the treatment of mortality rates in exploited fish populations.

	<12 mm	12–14 mm	14–18 mm	>18 mm
Low predation (M)	0.0297 (165)	0.0116 (143)	0.0106 (331)	0.0097 (278)
High predation ($F + M$)	0.0454 (424)	0.0251 (127)	0.0285 (280)	0.0251 (127)
Estimated F	0.0157	0.0135	0.0179	0.0154
$F/(F + M)$	0.35	0.54	0.63	0.61

Note: We treat low-predation sites as equivalent to an unexploited fish population so that the instantaneous mortality rates represent natural mortality (M). The high-predation sites are treated as equivalent to an exploited fish population, since they bear the additional mortality caused by predators ($F + M$). The difference between the two thus represents the increment in mortality caused by predation (F), which is then scaled by the total mortality rate for purposes of comparison with data from commercial fish populations. The two smaller size-classes are immature. The 14–18 mm size-class includes all mature males and females that are giving birth for the first time. The >18 mm size-class includes only females that are giving birth to subsequent litters. The numbers in parentheses are the numbers of marked and released fish.

Fig. 5. Frequency distribution of mortality ($F/(F + M)$) values for commercially exploited populations of fish (data from Fig. 1 of Mertz and Myers 1998). The histogram plots the mean values for three categories of exploited fish represented in their figure: heavily exploited groundfish (cross-hatched bars), pelagics (open bars), and other species (solid bars). We overlay the value of $F/(F + M)$ estimated for adult guppies (*Poecilia reticulata*) from our mark–recapture data.



purposes of comparison with data from commercial fish populations (Table 2). This treatment of the data demonstrates that the effects of predators on guppies are similar to the effects of fishermen on commercial fishes because the added mortality is greater in the larger, sexually mature size-classes (14–18 and >18 mm).

Since similar estimates of F and M are available for large numbers of commercially exploited populations of fish (Mertz and Myers 1998), it is possible to make direct comparisons between the added mortality attributable to predation on guppies with the mortality attributed to fishermen on commercially exploited fish (Fig. 5). For the purposes of comparison, we have plotted a value of 0.6 for guppies, which represents the approximate value for F on sexually mature individuals, since Mertz and Myers (1998) presented estimates of F for mature fish (Fig. 5). This comparison demonstrates that predator-induced mortality in guppies is comparable with, and most often lower than, fishing-induced mortality in commercial fisheries. Since the intensity of selection of life history traits will be directly proportional to the added mortality (Falconer and Mackay 1996), this comparison predicts similar patterns of life history evolution in commercially exploited fish populations but perhaps at a higher rate of change.

Table 3. Estimated rates of evolution in guppies (*Poecilia reticulata*) from the El Cedro River introduction experiment.

	No. of generations	Response	Rate (haldanes)
Males (4 years)			
Age	7	12.1 days	0.164
Size	7	6.4 mg	0.106
Females (7.5 years)			
Age	13	4.6 days	0.041
Size	13	10.3 mg	0.024

Note: The number of generations is based on estimates derived from mark–recapture studies and the amount of time between when guppies were transplanted from a high- to a low-predation locality and when we collected the grandmothers of the second-generation fish that were evaluated in the laboratory life history assay. "Response" is the difference in the age or size at sexual maturity in the second-generation descendants from the introduction and control sites. All of these differences were derived from fish that were reared in isolation on controlled levels of food availability and all are statistically significant (Reznick and Bryga 1987; Reznick et al. 1990, 1997). "Rate" is the rate of change estimated as the number of standard deviation units per generation, which is also called the haldane (Hendry and Kinnison 1999).

How long would it take for such evolution to occur? We can estimate the rate of evolution and the amount of time required for evolution in guppies from our introduction experiments. If we use the number of generations as a standard for evaluating rate, then it is possible to make predictions about rate of change in other organisms. It is also possible to predict, at least approximately, the amount of time it should take for such change to occur when we convert generations back into years.

Our highest resolution for evaluating the rate of evolution of guppies comes from our introduction experiment on the El Cedro River where we collected guppies from a high-predation site below a barrier waterfall and introduced them into a site above the barrier waterfall that previously only contained *R. hartii*. We compared the life histories of the introduction and control populations after 4 years (Reznick and Bryga 1987) and found that male age and size at matu-

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rity had changed to values that are typical of low-predation localities but that there had been no change in the female life history. We compared the introduction and control populations again, after 7.5 years, and this time found that there were also some changes in the age and size at maturity in females (Reznick et al. 1990). The differences in the rate of evolution of male and female traits were caused primarily by males having much higher heritabilities for age and size at maturity (Reznick et al. 1997). We estimated generation time in low-predation sites from our mark–recapture studies (Reznick et al. 1996*a*) and associated life history data (Reznick et al. 1997). We can thus report the rates of evolution in "haldanes", which equal the number of standard deviation units of change in the mean value of a trait per generation (Hendry and Kinnison 1999). This unit provides a frame of reference that is readily applied to other organisms, since it scales the rate of change in generations rather than years and hence accommodates differences in life cycles.

The magnitudes of the changes reported here (Table 3) represent a 5–15% increase in the mean age or size at maturity in the introduced populations after 7–12 generations of selection. For the sake of argument, we will assume that an equivalent number of generations is required for commercially exploited populations of fish to show equivalent changes in the life history. Sample generation times for commercially exploited fish range from 1 year for an anchovy (Peruvian (*Engraulis ringens*)) to 2 years for a salmon (pink (*Oncorhynchus gorbuscha*)), 5–8 years for a plaice (North Sea (*Pleuronectes platessa*)), 12 years for a cod (Atlantic (*Gadus morhua*)), and 15 years for a halibut (Atlantic (*Hippoglossus hippoglossus*)) (R. Myers, Department of Biology, Dalhousie University, Halifax, NS B3H 4A1, Canada, personal communication). This means that the time required for a 5%–15% change would take on the order of 10 years for an anchovy, 80 years for a plaice, and 120 years for a cod. Since many of these fish experience an added increment of mortality that is far greater than that exerted by predators on guppies (Fig. 5), we might expect them to evolve more quickly than guppies.

The actual rates will of course be a function of other factors, including the heritabilities of the traits in each population, the combination of direct and indirect effects of predators, the patterns of gene flow among different stocks of fish, and differences in the level of fishing-induced mortality in the different stocks. In spite of these complexities, the actual results in the few cases where we have good empirical data show that the appearance of change in exploited fish populations is consistent with the changes that we see in guppies and that the rate of change is often faster than estimates based on the above comparisons (Ricker 1980; Rijnsdorp 1991; Olsen et al. 2004). It is thus reasonable to argue that the phenotypic changes and age and size at maturity seen in commercial fisheries are caused by life history evolution.

What are the consequences of such evolution? Law (2000) summarized the application of life history theory to commercially exploited fish populations and the empirical evidence that some exploited populations have shifted towards earlier ages and smaller sizes at maturation. One consequence of the shift to smaller body size is that it will reduce yield. For example, Rijnsdorp (1993) estimated that there has been a 5% loss of yield in *P. platessa* as a consequence of such changes. Conover and Munch (2002) showed experimentally that the selective removal of larger individuals will select for the evolution of a smaller size at maturity and reduced growth rates. Likewise, evaluation of long-term trends in the North Sea also reveal an increase in small species with faster growth and earlier maturity and a decrease in slower growing species with late maturity (Jennings et al. 1999).

Law's (2000) models also predict that populations will evolve earlier maturity and smaller sizes under increased mortality rates much more readily than they will evolve delayed maturity at a larger body size when the mortality rate declines. The slower reversal is predicted because the intensity of selection for the reversion to the former life history will be weaker than the intensity of selection under added mortality. Said differently, the deleterious effects of life history evolution on yield will be slow to reverse when fishing pressure is reduced. Our experiments on guppies imply that the evolutionary impact of fishing can be reversible, since we selected for earlier maturity and smaller size when we added predators (Reznick et al. 2001*a*) and later maturity at a larger body size by introducing guppies into low-predation environments (Reznick et al. 1990, 1997). Likewise, Haugen and Vollestad (2001) and Olsen et al. (2004) observed reversals in the life history phenotypes of natural, exploited populations of fish when fishing pressure was reduced. However, these studies do not provide estimates for the intensity of selection in either direction or the comparative rates of evolution, so they do not provide a means of evaluating Law's theoretical results.

The effect of fishing on life history evolution is less predictable in models that embed the interaction between fishing and the life history evolution of the target species in a more realistic ecological setting (Abrams and Rowe 1996; Gardmark et al. 2003; Matsuda and Abrams 2004). How the species evolves will be a function of the sort of mortality patterns induced by fishing, the natural sources of mortality, natural food resources consumed by the exploited fish species, and the way commercial fishing interacts with these other features of the environment. More generally, if we think of a prey species as being part of an ecological community and of harvesting as a new source of mortality that alters the interactions among the components of the community and potentially alters the physical structure of the community (e.g., damage to the substrate by trawling), then it is easy to imagine that the long-term effects of fishing will be difficult to predict. The evolutionary response of the target species will be a function of the relative strength of the direct effect of fishing versus all of the indirect effects that fishing has on other interactions in the community. A positive aspect of such evolutionary considerations is that it is possible to design harvest regimes that can minimize life history evolution (Heino 1998). A negative aspect of such considerations is that the added mortality associated with commercial fishing might also cause a shift in community structure that could preclude the reestablishment of a depleted fish stock (De Roos and Persson 2002). Such shifts in community structure might explain Hutchings' (2000, 2001) and Hutchings and Reynolds (2004) analyses, which show that the populations of marine fish that have crashed as a re-

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sult of commercial fishing have failed to recover when fishing is reduced or stopped entirely.

One general conclusion from this sort of study is that evolution can be rapid enough to be an integral part of ecological interactions. Traditional fisheries management has implicitly assumed that this is not the case by modeling the effects of fishing on the basis of population dynamics alone. A more specific conclusion is that the effects of predators on guppies are similar to the effects of commercial fishing in terms of the added increment of mortality and because the added mortality is higher for the older, larger fish. The rate of evolution of guppies under such added mortality suggests that species that are subject to commercial exploitation should show similar patterns of evolution (earlier maturity at a smaller size) in time intervals on the order of decades. The phenotypic changes that we have seen in some exploited populations may thus represent life history evolution rather than ones that are solely attributable to environmental causes. If exploited species have evolved, then such evolution would help to explain why the recovery of fish populations after a reduction in commercial fishing has been so slow, since genetic changes will be less readily reversible than environment-induced plasticity.

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Harvest selection, genetic correlations, and evolutionary changes in recruitment: one less thing to worry about?[1]

S.B. Munch, M.R. Walsh, and D.O. Conover

Abstract: Harvest selection may lead to detrimental evolutionary changes in exploited populations. Few studies have considered the indirect impacts that harvest selection may have arising through genetic correlations. Using data from a long-term fishing experiment on Atlantic silversides (*Menidia menidia*), we show that there are significant genetic correlations between adult length at harvest and several early life history characters known to influence recruitment success. Based on this analysis, we estimate the magnitude of the change in recruitment success that may arise indirectly from selection on adults. In contrast with studies of harvest selection on adult characteristics, we find the response of characters in the early life history to be relatively slow and that impacts on recruitment, if any, are likely to be driven by selective changes in fecundity.

Résumé : La sélection due à la récolte peut mener à des changements évolutifs nocifs dans les populations exploitées. Peu d'études ont examiné les effets indirects que la sélection due à la récolte peut avoir par le biais des corrélations génétiques. À l'aide de données provenant d'une expérience à long terme sur les capucettes (*Menidia menidia*), nous démontrons qu'il existe des corrélations génétiques significatives entre la longueur des adultes à la récolte et plusieurs caractéristiques des premières étapes du cycle biologique, caractéristiques connues pour influencer le succès du recrutement. À partir de cette analyse, nous estimons l'importance du changement dans le succès du recrutement qui peut survenir indirectement par la sélection faite sur les adultes. Contrairement aux études faites sur la sélection due à la récolte sur les caractéristiques adultes, nous trouvons que les réactions des caractères des premières étapes du cycle biologique sont relativement lentes et que les impacts sur le recrutement, s'il y en a, sont vraisemblablement causés par des changements sélectifs de la fécondité.

[Traduit par la Rédaction]

Introduction

There is growing concern that the selective effects of harvest may lead to detrimental evolutionary changes in life history characters (e.g., see Stokes et al. 1993). This concern is well founded, given the magnitude and size-selective nature of fishing mortality (Hanson and Chouinard 1992; Kristiansen and Svasand 1998) and the rapid evolution of life histories in natural fish populations (Reznick et al. 1990; Haugen and Vøllestad 2001). Significant changes in size and age at maturity have been observed in several heavily exploited stocks (Rijnsdorp 1993; Rochet 1998; Grift et al. 2003). In addition, several species have shown significant decreases in size at age, attributed primarily to evolution in response to harvest (Ricker 1981; Harris and McGovern 1997; Sinclair et al. 2002*b*). Since harvest selection is typically directed at mature individuals, most studies of fisheries-induced adaptive change have focused on production traits of adults, such as size and age at maturity. The potential for harvest selection to affect traits expressed earlier in the life history remains largely unstudied.

Recruitment variability is the most important source of uncertainty in managing fish populations (MacKenzie 2000; Rothschild 2000). Nearly 90% of a cohort may be lost during early life stages. Recruitment success has been linked to egg size (Rijnsdorp and Vingerhoed 1994), larval size at hatch, and growth through larval (Pepin and Myers 1991; Pepin 1993; Houde 1997) and juvenile stages (Sogard 1997). Variation in these traits among individuals is largely thought to be determined by environmental variation (e.g., Houde

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S.B. Munch.[2] Center for Stock Assessment Research and Jack Baskin School of Engineering, Department of Applied Mathematics, University of California, Santa Cruz, CA 95064, USA.
M.R. Walsh and D.O. Conover. Marine Sciences Research Center, State University of New York at Stony Brook, Stony Brook, NY 11794-5000, USA.

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[2]Corresponding author (e-mail: sbmunch@soe.ucsc.edu).

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1987). In addition to predation, food availability (e.g., Cushing 1990), larval transport (Dalley et al. 2002), and turbulence (Rothschild and Osborn 1988) are among the many environmental factors thought to influence recruitment success.

The genetic basis of characters expressed early in the life history of fishes is largely undocumented. Consequently, the potential for genetically based changes in recruitment success has thus far been ignored. We have recently shown that artificial selection on adult size resulted in nonrandom, genetically based changes in juvenile size at age (Conover and Munch 2002; Munch et al. 2004). Since mortality through the juvenile stage is size dependent, we might therefore expect harvest selection on adult size to cause genetically based changes in recruitment.

Here, we reanalyze data from a long-term selection experiment on Atlantic silversides (*Menidia menidia*) (Conover and Munch 2002; Walsh 2003; Munch et al. 2004) and show that there are significant genetic correlations among adult traits and several early life history characters known to influence recruitment success. We briefly review the literature on the size dependence of mortality during the egg, larval, and juvenile stages to construct a size-based model of survival. Using this model, we evaluate the magnitude of the changes in recruitment per egg that can be expected from the selective removal of adults.

Methods

To estimate the expected change in recruitment resulting from selection on adult size, we need two things. First, we must have a means of estimating the expected change in early life history characters resulting from selection on adults. The experimental design described below provides information on genetic variance of, and covariance with, length at harvest. Using these data to estimate heritability and coheritability (see Analysis and modeling section), we may make predictions of the evolutionary response of early life history traits to a single generation of selection on adult length. Second, we must have a model representing mortality as a function of each of the early life history characters that we measured. To this end, we reviewed the literature on survival as a function of egg diameter and length in larvae and juveniles.

Selection responses of correlated characters

To evaluate the selective effects of harvest on adult size and correlated life history characters, we conducted a long-term selection experiment using Atlantic silversides. The Atlantic silverside is a small, shallow-water atherinid found in estuaries throughout the eastern coast of North America from Florida, USA, to New Brunswick, Canada. Silversides have a simple annual life cycle: at all latitudes, all fish in wild populations mature at age 1 and are locked into doing so by the annual sequence in photoperiod. Given this constraint on silverside life history, our selection experiment focused on fishery-induced changes in size at age rather than age at maturity. Detailed descriptions of the design and primary results of the selection experiment have been published elsewhere (Conover and Munch 2002) and are only briefly reviewed here.

We established three kinds of experimental fisheries: (*i*) those in which only the largest fish were taken (largest 90% harvested), (*ii*) those in which only the smallest fish were taken (smallest 90% harvested), and (*iii*) those in which the fish were removed from the population randomly with respect to size (90% randomly harvested). Each of these experimental fisheries was replicated twice for a total of six independent experimental lines. To prevent loss in case of disease outbreak or system failure, we reared fish for each line in two independent, duplicate phases of approximately 500 fish each. Harvest occurred at the adult stage (190 days postfertilization) approximately 1 month prior to spawning. Each fishery was carried out for a period of five generations.

Recruitment in each phase of this experimental fishery was standardized in two stages. Initially, eggs deposited on spawning mops over a 1- to 3-day period were transferred into and allowed to hatch in rearing containers. On about day 30, after the initial larval mortality had subsided, 175 larvae from each of four to six birthdates spanning 1–2 weeks were transferred into rearing buckets. These 2-week birthdate intervals for each phase were taken from approximately the middle of the spawning period to ensure maturation of all potential spawners. A second density reduction occurred at 90 days of age when 550 juveniles, sampled uniformly from the rearing buckets, were transferred into larger aquaria for the remainder of the life cycle. Care was taken at both of these culling stages to ensure that the counting process was not size selective. Thus, recruitment for each population consisted of about 1000 fish at the time of harvest.

Some readers may question the adequacy of this experimental design as a simulation of fishing in wild populations. We acknowledge that the experiment differs significantly from real fisheries in several regards. First, recruitment is standardized. Consequently, density-dependent effects could have occurred only in the egg and early larval period and cannot be estimated from this design. Second, there are no predators. Consequently, apart from uncontrolled mortalities occurring from unknown causes, there is no natural selection acting to oppose the selection regime imposed by harvest. However, these apparent shortcomings are, in fact, the controls that allow us to accurately disentangle genetic from environmental influences on growth and other characters. As an experiment to estimate realized heritability for size at age, this experimental design is nearly ideal (Falconer and Mackay 1996). Finally, although it is expected that growth in the field may be quite different from that observed under laboratory conditions, it is the heritability of size, i.e., the fraction of variation in size attributable to additive genetic effects (see Analysis and modeling section), rather than size per se that is important. Estimates of the heritability of similar life history characters do not differ significantly between the laboratory and field (Weigensberg and Roff 1996).

Egg size, larval size at hatch, and larval survival were also measured. Egg diameters were measured for generations 3 through 5 on random samples of 30 eggs per experimental fishery (Walsh 2003). Larval size at hatch (total length) was measured for thirty 1-day-old larvae from each fishery in generations 4 and 5 (Walsh 2003). For the first generation prior to selection and generations 2 through 4, length at age 15 days was measured for 40–50 individuals from each fishery. All eggs and larval lengths were measured by ocular mi-

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crometer (nearest 0.01 mm). Juvenile length at age was measured (nearest millimetre) every 20 days from age 90 to 190 days for fish in generations 3 through 5 on groups of 40–70 individuals sampled from each line (Conover and Munch 2002).

Posthatch larval survivorship was estimated on three batches of 50 larvae per experimental fishery (generation 5) fed ad libitum for 10 days posthatch (Walsh 2003). From these data, larval viability was calculated as $-\ln(N_{t_{end}}/N_{t_{start}})/10$.

Analysis and modeling

Our experimental design provides information on the genetic variance of and covariance with adult length (i.e., length at 190 days) from which we may make predictions of the evolutionary response of early life history traits to a single generation of selection on adult length. Heritability (h_x^2) is defined as the expected change in mean phenotype of offspring in response to a unit of selection applied to parents (Fig. 1). In other words, it is the fraction of a change in the mean phenotype of parents that will be transmitted to offspring and may estimated as the slope of the regression of offspring phenotype on parent phenotype. More formally, the response of a trait to selection is given by the breeder's equation

$$\Delta R_x = h_x^2 \Delta S_x \quad (1)$$

where the response to selection (ΔR_x) is defined as the observed difference between the mean offspring phenotype for trait x and that of the entire prior generation, while the selection differential (ΔS_x) is defined as the difference in mean phenotype of parents (i.e., the subset of the prior generation allowed to reproduce) and that of the entire prior generation.

Similarly, coheritability ($h_{x,y}$) is proportional to the additive genetic covariance among traits and, as the name implies, is related to the expected change in a trait that results from selection on another trait. As above, coheritability may be estimated as the slope of the regression of offspring phenotype on parent phenotype for another trait. (Here, we depart slightly from the definition for coheritability given in Falconer and Mackay (1996) to simplify the notation.) Formally, the change in a trait (y) resulting from selection on trait x is given by

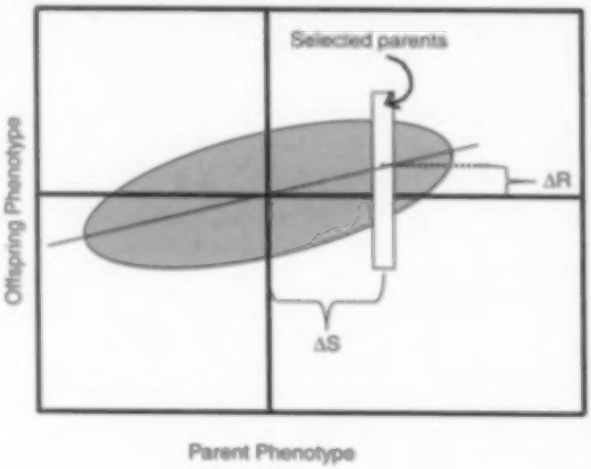
$$\Delta R_y = h_{x,y} \Delta S_x \quad (2)$$

Heritability and coheritability may be also estimated from selection experiments conducted over several generations (Falconer and Mackay 1996). In this case, the estimates are referred to as realized heritability and realized coheritability to distinguish them from their single-generation counterparts. Realized heritability (coheritability) is estimated by linear regression of the response to selection (as defined previously) on the cumulative selection differential. The cumulative selection differential at generation n ($\Delta S_{x,n}$) is defined as the sum of the single-generation selection differentials applied up to the present:

$$\Delta S_{x,n} = \sum_{i=1}^{n} \Delta S_{x,i} \quad (3)$$

To account for variance due to drift and unintended changes in the environment, we used a general linear model

Fig. 1. Heritability illustrated. The ellipse indicates the bivariate distribution of parent and offspring phenotypes. The slope of the regression line passing through this distribution is the heritability (h^2) or the fraction of a change in parent mean expected to be transmitted to offspring. The line gives the mean phenotypes of parents and offspring in the absence of selection. The rectangle indicates the range of parent phenotypes allowed to reproduce in a putative selection experiment. ΔS is the selection differential or difference in mean between selected and unselected parents. The expected change in the mean offspring phenotype is indicated by ΔR and is given by the breeder's equation $\Delta R = h^2 \Delta S$.



approach as follows. The vector of offspring mean length at harvest ($\boldsymbol{L}_{190}$) for each line at each generation was modeled as

$$\boldsymbol{L}_{190} = \mu + \beta \mathbf{X} + h_{190}^2 \Delta \boldsymbol{S}_{x,n} + \varepsilon \quad (4)$$

where μ is the mean, h_{190}^2 is the heritability of length at 190 days of age, $\Delta \boldsymbol{S}_{x,n}$ is the vector of cumulative selection differentials, and ε is a normally distributed error term accounting for drift variance, measurement error, and nonadditive genetic effects (see Falconer and Mackay (1996) for more details). Here, $\mathbf{X}$ is a design matrix accounting for the effects of generation and phase. Specifically, the generation effect is simply a deviation from the grand mean common to all lines within a given generation. Similarly, the phase effect is a deviation from the generation mean common to all lines within a specific rearing phase. Thus, with the inclusion of the term $\mu + \beta \mathbf{X}$, eq. 4 is equivalent to an analysis of covariance (in which cumulative selection is the covariate) with phases nested within generations (McCulloch and Searle 2001). Coheritabilities were also estimated using eq. 4, by replacing $\boldsymbol{L}_{190}$ with vectors of mean egg diameter, larval viability, and length at age and modifying the design matrix to include only those generations and phases for which these traits were measured.

To predict changes in the size trajectory at ages other than those explicitly measured, we need an estimate of the coheritability function $h(L_{190}, L_t)$. Here, L_{190} is length at 190 days and L_t is length at some prior age (t). An estimate of the coheritability function may be obtained by fitting a

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smooth function to the individual coheritability estimates (Kirkpatrick and Lofsvold 1989):

$$(5)\qquad h(L_{190},L_t) = h^2 \exp[-p_1(190-t)^2 - p_2(190-t)]$$

where h^2, p_1, and p_2 are coefficients that we estimated by nonlinear least squares from the coheritability values for each age, assuming additive normal errors.

We define recruitment per egg as survival from egg to age at harvest (190 days) and divide the life history into two distinct mortality stages, egg and larval–juvenile. In both stages, we model relative survival, defined as survival after a single generation of selection applied to adults divided by survival in the absence of selection. We assume that mortality through the egg stage declines exponentially with egg diameter (D) and is constant from fertilization until hatch. Parameters are drawn from Rijnsdorp and Vingerhoed (1994). Note that these parameters are for sole and may not apply directly to *M. menidia*. To our knowledge, however, estimates of the size dependence of egg mortality for *Menidia* or closely related species are unavailable. Rijnsdorp and Vingerhoed (1994) modeled mortality as $\ln M = a + bD + cT$ and reported values of $a = -0.075$ (±0.611), $b = -2.016$ (±0.251), and $c = 0.173$ (±0.039). We assume that temperature (T) over the 7-day egg stage is constant at 15 °C, the temperature at which silversides begin spawning, and combine their parameters a and c to give

$$(6)\qquad S = \exp[-m_e \exp(bD)t_h]$$

where S is survival through the egg stage, $\ln m_e = 2.52 \pm 0.85$ with a standard error of $S_e^2 + (15\ \mathrm{SE})^2)^{1/2}$, $b = -2.016$, and t_h is the duration of the egg stage (age at hatch = 7 days). Note that the error estimate for m_e includes measurement and process uncertainties and is likely to be considerably larger than an interval estimate based on process errors alone.

As described above, the change in egg diameter resulting from a selective change in length at harvest is given by $\Delta D = h(L_{190}, D)\Delta L_{190}$. Consequently, survival through the egg stage after selection, expressed as a fraction of survival in the absence of selection, is given by

$$(7)\qquad S_E = \exp[m_e t_h(\exp(-bD) - \exp\{-b[D + h(L_{190},D)\Delta L_{190}]\})]$$

Recruitment is also affected by changes in larval viability as assayed by the larval survival experiments. The viability mortality rate V resulting from selection on adults is given by $V = \bar{V} + h(L_{190},V)\,\Delta L_{190}$ where $\bar{V}$ is the mean mortality rate for an unselected population. Consequently, changes in viability, S_V, resulting from selection were modeled as

$$(8)\qquad S_V = \exp[-h(L_{190},V)\Delta L_{190} t_l]$$

where t_l is the duration of the larval period and is assumed constant at 10 days. Note that the mean viability cancels when calculating relative survival so that S_V is insensitive to uncertainty in the mean mortality rate.

Survival from hatching to harvest is, in part, length dependent. Specifically, we consider mortality through the growing season as a sum of length-dependent and length-independent components. Assuming that the components of mortality that do not depend on length are the same for selected and unselected populations, this additional mortality will cancel in the calculation of relative survival and can, for present purposes, be ignored. Based on our review of the literature, the length dependence of mortality during the larval and juvenile stages is modeled as a power function of length. Thus, the component of survival from hatching to harvest that depends on length is given by

$$(9)\qquad S = \exp\left(-m_j \int_{t_h}^{t_r} L_t^d \,\mathrm{d}t\right)$$

where t_r is the age at recruitment, held constant at 190 days. Here, L_t is the mean size at time t in the absence of selection for ages t_h to t_r. Since there are no adequate field estimates of silverside mortality as a function of length, the parameters m_j and d were estimated by linear regression of values of $\ln M$ on $\ln L$ (Fig. 2) obtained from Rilling and Houde (1999), Palomera and Lleonart (1989), Pertierra (1992), Crecco et al. (1983), Dey (1981), and sources cited in Adams et al. (1996). Parameters for the length dependence of mortality for larvae and juveniles were $\ln m_j = 0.478$ (±0.636) and $d = -1.125$ (±0.203). Since these estimates are based on a regression of point estimates for a variety of species, the error bounds incorporate process uncertainty, measurement errors, and variation among species. The error bounds are thus likely to be substantially greater than a *Menidia*-specific process error interval and, within these bounds, our results for length-dependent mortality should be fairly robust. The L_t in the absence of selection was estimated as a second-order polynomial from the mean growth trajectories of fish in the random harvest lines in generations 3 through 5. Specifically

$$(10)\qquad L_t = 0.002t^2 + 0.047t + 4.631$$

which describes the mean growth trajectory of unselected silversides quite well ($R^2 = 0.99$). Changes in length at age resulting from selection on adults were given by the coheritability function as $\Delta L_t = h(L_{190}, L_t)\Delta L_{190}$. Consequently, the relative survival S_J is given by

$$(11)\qquad S_J = \exp\left(-m_j \int_{t_h}^{t_r} L_t^d - [L_t + h(L_{190},L_t)\Delta L_{190}]^d \,\mathrm{d}t\right)$$

This integral was evaluated numerically using a daily time step over the period t_h to t_r.

The overall recruitment per egg (S_T) resulting from a round of selection on adults expressed as a fraction of recruitment in the absence of selection is given by

$$(12)\qquad S_T = S_E S_V S_J$$

We modeled the relative survival of each stage using several different selection differentials. We used a selection differential of 10 mm, comparable with what was applied in our harvest selection experiment. We also used several values closer to those observed in actual fisheries. Law and Rowell (1993) estimated selection differentials for age-1 North Sea cod on the order of about –0.24 cm over a 3-month period or about –0.99 cm annually. Expressed in standard deviation units, this is equivalent to a standardized selection differential of –0.19.

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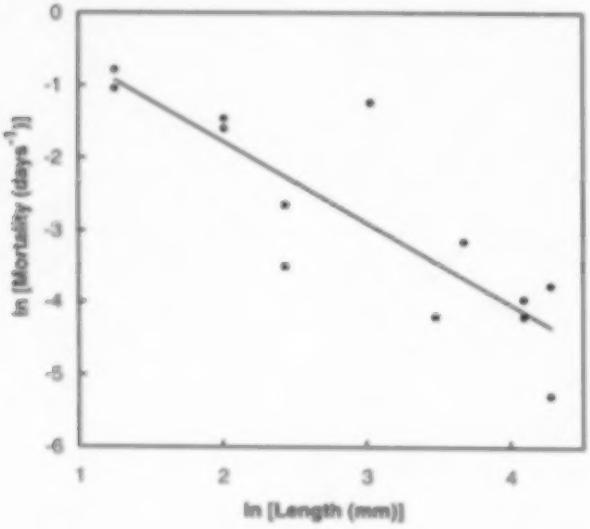
Fig. 2. Published values of ln(mortality) versus ln(length) for larvae and juveniles. This figure includes values from Rilling and Houde (1999), Palomera and Lleonart (1989), Pertierra (1992), Crecco et al. (1983), Dey (1981), and sources cited in Adams et al. (1996).



Since the phenotypic standard deviation for length at harvest in *M. menidia* is 8.25, a selection differential comparable in magnitude with that of the cod fishery would be –1.6 mm. Relative survival was also assessed for selection differentials of 1, 2, and 3 mm. Sensitivity to the parameter estimates used in modeling was assessed by calculating relative survival using the upper and lower confidence bounds for each of the mortality parameters.

Results

Correlated characters

Selection on length at 190 days resulted in significant changes in egg diameter and larval viability (Walsh 2003). There were also significant changes in length at all ages (Table 1) (Conover and Munch 2002; Walsh 2003). In each case, the offspring of large-size harvested lines were smaller or less viable than offspring of the random- and small-size harvested lines. Curiously, lengths of larvae at age 15 days showed the opposite pattern; the large-size harvested lines were somewhat larger, although the differences were not significant. We expect that the absence of significant coheritability at 15 days is a result of the relatively small sample size used at this stage rather than an intermediate period during which the genetic correlation with adult size is reversed. The estimated realized coheritability function was highly significant ($R^2 = 0.99$, $p < 0.001$) (Fig. 2) with parameters $h^2 = 0.183$ (±0.005), $p_1 = 0.0001$ (±0.000 03), and $p_2 = 0.004$ (±0.0020). Thus, selection applied to length at 190 days had significant effects on length at all ages, the magnitudes of which increased with age.

Realized coheritability for egg diameter was 0.0006 (±0.000 04) ($p < 0.0001$). Since egg diameter was significantly correlated with maternal length ($r = 0.84$, $p < 0.001$), an obvious question is whether the observed variation in egg diameter is simply an effect of maternal size. We addressed this issue by including the mean length of parents at 190 days as an additional covariate in the generalized linear model to estimate coheritability. Here, mean length of parents is simply the adult length (i.e., on day 190) of the fish that were allowed to spawn rather than the mean size of the entire population. The estimated effect of parent length on egg diameter was marginally nonsignificant (slope = 0.0005 ± 0.000 23, $p = 0.06$). More importantly, the estimate of coheritability remained highly significant ($p = 0.0003$), indicating that selection on adult size resulted in significant genetic changes in egg diameter independent of maternal size effects. There were no significant phenotypic correlations between mean parent length and other early life history characters. Further, there were no significant phenotypic correlations between egg diameter and any other early life history character, although the correlation between egg diameter and larval length at hatch was only marginally nonsignificant ($r = 0.54$, $p = 0.07$). Thus, differences among selected lines in early life history traits are a direct consequence of genetic correlations with adult size. Coheritability for larval viability (0.0009 ± 0.0004) was marginally nonsignificant ($p = 0.06$).

Table 1. Age-specific coheritability estimates based on the generalized linear model described in this study.

Age (days)	Coheritability with length at 190 days	R^2	p
7	0.004 (0.0008)	0.677	0.001
15	–0.005 (0.0030)	0.140	0.125
90	0.046 (0.0038)	0.901	<0.001
111	0.063 (0.0079)	0.795	<0.001
133	0.094 (0.0098)	0.853	<0.001
153	0.138 (0.0092)	0.933	<0.001
174	0.169 (0.0099)	0.947	<0.001
190	0.182 (0.0106)	0.913	<0.001

Note: The numbers in parentheses are standard errors for the regression coefficients.

Effects on recruitment

We found that using the mean values of the mortality parameters resulted in negligible reductions in survival as a consequence of selection (Table 2). For all selection differentials applied, the expected survival through each of the stages was never less than 88% of that expected in the absence of selection. Selection on adult size produced the greatest decrease in survival through the egg stage. Approximate confidence intervals for relative survival through each stage were obtained from the confidence intervals for the mortality parameters. For a selection differential of –1.6 mm, comparable with that in the North Sea cod fishery, we found a lower bound on relative egg survival of 87% and relative survival through the larval–juvenile stages of 79%. For the selection differential applied to our simulated fishery (–10 mm), the lower bound estimates of relative survival through these stages were 43% and 22%, respectively.

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Table 2. Relative survival estimates.

Selection differential (mm)	Standardized selection differential	Egg survival ratio	Viability survival ratio	Hatch to harvest survival ratio
−1.6	−0.19	0.981 (0.874, 0.997)	0.98	0.986 (0.787, 0.999)
−10	−1.21	0.886 (0.430, 0.984)	0.91	0.915 (0.220, 0.995)
−1	−0.12	0.988 (0.919, 0.998)	0.99	0.991 (0.861, 1.000)
−2	−0.24	0.976 (0.845, 0.997)	0.98	0.983 (0.741, 0.999)
−3	−0.36	0.965 (0.777, 0.995)	0.97	0.974 (0.638, 0.999)

Note: Columns 1 and 2 give the modeled selection differential and standardized selection differential. Columns 3–5 give the survival of offspring of selected parents through each stage relative to expected survival in the absence of selection. In columns 3 and 5, the numbers in parentheses are ranges based on the confidence intervals for the mortality parameters. As noted in the Methods, uncertainty in viability cancels in the calculation of the survival ratio.

Discussion

Recruitment studies typically focus on the characteristics of larvae and juveniles independent from the rest of the life history. Here, we have demonstrated that there are significant genetic correlations between adult length and several early life history characters known to influence recruitment. We found significant estimates of coheritability for egg diameter, length at hatch, and length from ages 90 to 190 days. At least qualitatively, our estimated coheritability function for length at age (Fig. 3) is quite similar to the appropriate cross section of the genetic covariance function estimated by Kirkpatrick (1993) for rainbow trout, implying that this pattern of genetic covariation among lengths at age is a general phenomenon.

One cause for concern in this type of analysis is that the results may be artifacts caused by maternal effects or phenotypic correlations that result simply from the amplification of early differences in growth. In the first case, we should expect to find that the traits in question are more strongly correlated with maternal length than the cumulative selection differential. However, of the traits measured, only egg size was significantly correlated with maternal length at 190 days. Moreover, we found that after statistically controlling for the influence of selection, this correlation was no longer significant. In the second case, we would expect that size at age would be more strongly correlated with egg size or size at hatch than with the cumulative selection differential. No significant correlations with egg diameter or hatch length and length at subsequent ages were found. Consequently, we conclude that there are genetic contributions to egg size, length at hatch, and length at subsequent ages that share genetic correlations with length at 190 days.

Based on our review of the mortality literature, we found that mortality appears to scale approximately inversely with length during the larval and juvenile periods. Several previous authors have reached similar conclusions regarding the length dependence of mortality (Petersen and Wroblewski 1984; McGurk 1986; Pepin 1993). Note that the size dependence exponent generated from data across several species (−1.125) is very close to those obtained by Lorenzen (1996) for mortality within species (mean −1.69, range −0.6 to −5.21, after excluding a single outlying value of −24.58 for *Stizostedion vitreum* from East Okerboji Lake). This suggests that the length allometry of mortality is fairly robust, although there may be considerable variation in mortality from other sources. Given that mortality is length dependent, that growth through the larval stage is thought to be an important determinant of recruitment success, and that there are significant genetic correlations between sizes early and late in the life history, we expected to predict that selection on adult size would produce substantial changes in recruitment. However, our models revealed that despite significant genetic correlations between early life history characters and adult size, harvest selection is likely to have a negligible effect on recruitment per egg. This result is a consequence of two facts. The first is that the published selection differentials that are imposed by fisheries are fairly small (Law and Rowell 1993). The second is that the mortality and coheritability functions have opposing trends that tend to negate each other. That is, fisheries-induced genetic changes in length are greatest just prior to harvest when length-dependent mortality is negligible and least during the larval stage when length-dependent mortality is the most severe.

It is important to note that our results apply only to a single generation of selection on adult length. We estimate that it would take at least five generations of selection (using average parameter values and a typical fishery selection differential of −1.6 mm) to cause a 20% drop in recruitment as a consequence of cumulative changes in survival through all stages. Considering each stage alone, it would take 12 generations of selection on adults to cause a 20% drop in egg survival and 15 generations to cause a drop of similar magnitude in survival through the larval–juvenile period. These estimates assume that there is no selection acting directly on these early life history characters that would oppose the correlated response from harvest selection and should therefore be considered a minimum bound on the number of generations required. Actual responses of early life history characters to harvest selection may be quite a bit slower.

Although the impacts of selection on recruitment per egg appear to be fairly mild for reasonable selection differentials, it is of interest to estimate the severity of selection required to achieve a given reduction in recruitment per egg. With this in mind, we have calculated the expected relative survivorship for a broad range of selection differentials (Fig. 4). Conveniently, we found that these predictions are well approximated by a simple exponential model, $S_T = \exp(r\Delta S)$. Here, ΔS is the selection differential expressed in standard deviation units and $r = 0.16$ for the mean model. Using the mean model, we found that to generate a 40% reduction in survival from egg to adulthood, selection would have to shift the mean length of survivors by more than 3 SD. Although it may well be that the selection differentials

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Fig. 3. Realized coheritability function for length at age from hatch to harvest.

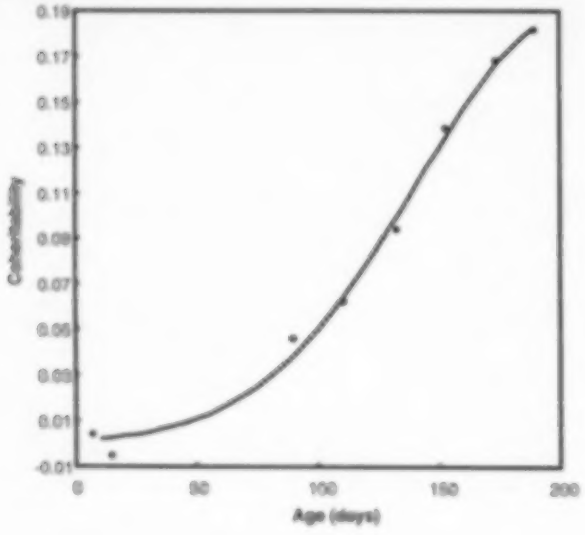
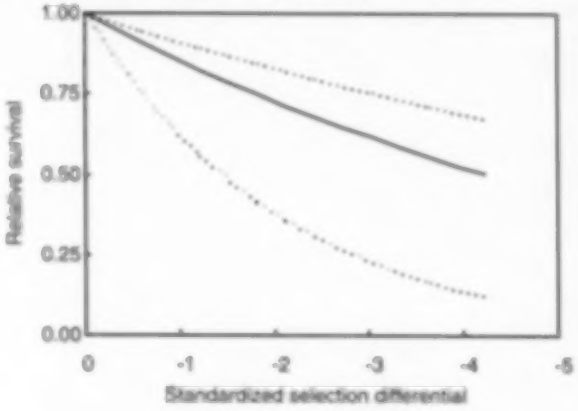


Fig. 4. Relative survival as a function of the selection differential. The horizontal axis in this figure is the reduction in mean length resulting from selection expressed in standard deviation units. The solid line shows the expected relative survival calculated as in eq. 12 for a broad range of selection differentials expressed in standard deviation units. The broken lines show the approximate confidence intervals based on upper and lower bounds for each of the mortality parameters.



imposed by fisheries are more severe than current estimates indicate, selection of this magnitude is exceedingly unlikely. However, after incorporating uncertainty from the various submodels, the approximate confidence bounds are quite wide: $r \approx 0.09$ and 0.49 for the upper and lower bound models. When evaluated at the lower bound, a 40% reduction in survival requires only a decrease in the mean of 1 SD. The published literature on fishery-imposed selection differentials is quite limited and estimating selection differentials are an important area of research if the evolutionary impacts of harvest are to be managed. The methods applied by Sinclair et al. (2002*a*) represent an important step in this direction.

In modeling changes in recruitment per egg, we have made two simplifying assumptions. First, we assumed that coheritabilities measured in the laboratory might be reasonably applied to wild populations. To our knowledge, there are no studies comparing coheritabilities estimated in the laboratory and field. However, indirect support of this assumption comes from Weigensberg and Roff (1996), who have shown that estimates of heritability do not differ among wild and laboratory populations. Second, we compared survival for average growth trajectories of offspring from populations with and without harvest selection. Since size at age typically varies among individuals, a more exact, although computationally daunting, approach would involve integrating mortality through time over distributions of size at age. As long as selection differentials are small, our approach will be a reasonable approximation to the full stochastic model. If selection differentials are large and there is substantial variability in length, our approach will tend to overestimate relative survival, since there will be a much greater fraction of the selected population's length distribution that is subjected to high mortality.

Since our models focus on recruitment per egg, they do not address changes in recruitment due to selective differences in fecundity. Fecundity strongly depends on body size, and selective removal of large, old individuals may change population productivity (Rochet 2000). In fact, we observed changes in fecundity in our experimental populations. By generation 4, large-size harvested populations produced only half as many eggs as small-size harvested fish. While we do not have sufficient information to determine whether this effect is genetic or simply an effect of maternal size, this distinction is not entirely relevant. Since we expect that selection on adults will produce evolutionary changes in maternal size, changes in fecundity are expected to occur whether the positive correlation with maternal size is genetic or purely phenotypic. Since the total number of individuals recruiting to a population is given by the number of eggs produced and the probability that these will survive to adulthood, proportional changes in fecundity would, in the absence of density effects on survival, produce proportional changes in recruitment. Thus, a twofold change in fecundity would far outweigh any of the effects on recruitment modeled here.

It is also worth emphasizing that the traits that we analyzed here were measured under ideal laboratory conditions of unlimited food and we have not measured the responses of these traits to gradients in density. It is certainly possible that different growth and life history genotypes will be selected for under food-limiting conditions of high density (Sokolowski et al. 1997) and that this may alter the pattern of coheritability reported here. Consequently, our results will be most directly applicable to populations at low densities such as those recovering from exploitation. Viewed in this light, our experimental reductions in viability and modeled reductions in survival foreshadow corresponding reductions in the intrinsic rate of increase for heavily harvested populations and concomitant increases in the time required for population recovery.

There have been a number of recent studies modeling the adaptive response of fish populations to harvest selection. Owing to a lack of relevant data, few of these have at-

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tempted to incorporate genetic covariance among traits. However, genetic covariance among traits may have important impacts on the response to selection, resulting in adaptive change along genetic lines of least resistance (Lande 1979). For instance, if there are strong genetic correlations among size at each age and selection during the early life history favors rapid growth, while harvest selection favors slow growth, size trajectories will evolve, but at rates lower than would be predicted for either trait alone. Consequently, the rates of evolution estimated using models of harvest selection that focus on single traits or ignore genetic correlations may be quite inaccurate. Given an estimate of the genetic covariance matrix, models like the ones we used may be generalized to include selective effects at other life stages (e.g., see Kirkpatrick (1993) for a description of the approach). Thus, an important next step in understanding the full life history implications of harvest selection is to estimate genetic covariances among life history characters (including growth trajectories) for exploited species.

This is the first paper to address the potential genetic impacts of selective fishing on early life history characters. We found that there were small but significant genetic changes in early life history characters that resulted from selection on adult size. In addition, although harvest selection appears to have substantial impacts on traits expressed in adults, our modeling results indicate that the expected response of early life history characters is much slower. Consequently, if significant changes in recruitment do result from harvest selection, our work suggests that they will be driven by changes in adult traits such as fecundity or age at maturity.

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Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*)[1]

Esben Moland Olsen, George R. Lilly, Mikko Heino, M. Joanne Morgan, John Brattey, and Ulf Dieckmann

Abstract: By estimating probabilistic reaction norms for age and size at maturation, we show that maturation schedules of Atlantic cod (*Gadus morhua*) off Labrador and Newfoundland shifted toward earlier ages and smaller sizes during the late 1980s and early 1990s, when these populations underwent a severe collapse in biomass and subsequently were closed for directed commercial fishing. We also demonstrate that this trend towards maturation at younger ages and smaller sizes is halted and even shows signs of reversal during the closure of the fisheries. In addition, our analysis reveals that males tend to mature earlier and at a smaller size than females and that maturation age and size decrease with increasing latitude. Importantly, the maturation reaction norms presented here are robust to variation in survival and growth (through phenotypic plasticity) and are thus strongly indicative of rapid evolutionary changes in cod maturation as well as of spatial and sex-specific genetic variation. We therefore suggest that maturation reaction norms can provide helpful reference points for managing harvested populations with evolving life histories.

Résumé : L'estimation de normes probabilistes de réaction pour l'âge et la taille à la maturation nous permet de démontrer que les calendriers de maturation de la morue franche (*Gadus morhua*) au large du Labrador et de Terre-Neuve ont glissé vers des âges plus précoces et des tailles plus basses au cours de la fin des années 1980 et du début des années 1990; à ce moment, ces populations ont connu un effondrement important de leur biomasse, après quoi il y a eu interdiction de la pêche commerciale ciblée. Nous démontrons aussi que la tendance vers une maturation à des âges plus précoces et à des tailles plus petites s'est arrêtée et a même montré des signes de retour en arrière durant la période d'interdiction de la pêche. De plus, notre analyse démontre que les mâles tendent à atteindre la maturité plus jeunes et plus petits que les femelles et que l'âge et la taille à la maturation décroissent en fonction de l'augmentation de la latitude. Il est important de noter que les normes de réaction de maturation que nous présentons sont robustes vis-à-vis la variation de la survie et de la croissance (via la plasticité phénotypique) et qu'elles indiquent ainsi fortement l'existence de changements évolutifs rapides dans la maturation des morues, ainsi que des variations génétiques en fonction de l'espace et du sexe. Nous croyons donc que les normes de réaction de la maturation peuvent fournir des points de référence utiles pour la gestion de populations exploitées à cycle biologique en cours de modification.

[Traduit par la Rédaction]

Introduction

There is accumulating evidence that significant evolutionary changes may occur on contemporary timescales in natural populations, often within just a few years or decades (Reznick et al. 1990; Hendry et al. 2000; Grant and Grant 2002). In some cases, such changes may be brought about by single episodes of particularly strong selection. For instance, the beak size of Darwin's finches (*Geospiza fortis*) on the Galapagos Islands evolved in response to a drought

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E.M. Olsen[2,3] and U. Dieckmann. Adaptive Dynamics Network, International Institute for Applied Systems Analysis (IIASA), A-2361 Laxenburg, Austria.
G.R. Lilly, M.J. Morgan, and J. Brattey. Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, NL A1C 5X1, Canada.
M. Heino. Adaptive Dynamics Network, International Institute for Applied Systems Analysis (IIASA), A-2361 Laxenburg, Austria, and Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway.

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[2]Corresponding author (e-mail: e.m.olsen@bio.uio.no).
[3]Present address: Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, P.O. Box 1066, Blindern, N-0316 Oslo, Norway.

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episode occurring within the timescale of one generation (Grant and Grant 2002). In the light of these findings, it has recently been argued that microevolution should be accounted for in the management of harvested populations and, more generally, in conservation biology (Stokes and Law 2000; Stockwell et al. 2003; Ferrière et al. 2004).

The populations of Atlantic cod (*Gadus morhua*) found off Labrador and Newfoundland in the Northwest Atlantic supported rich fisheries for hundreds of years (Templeman 1966; Hutchings and Myers 1995) but suffered a major decline in the early 1970s and a collapse in the late 1980s to early 1990s (Taggart et al. 1994; Myers et al. 1997). This collapse forced the Canadian government to close down much of the cod fisheries, and many coastal communities that used to depend on the cod experienced much economic and social hardship (Felt and Locke 1995). The moratorium on cod fishing has remained in effect in the areas that used to support the largest catches of cod (Lilly et al. 2003).

Evolutionary theory predicts that the heavy mortality imposed by industrial fisheries may cause evolutionary changes in exploited fish populations (Law and Grey 1989; Policansky 1993; Abrams and Rowe 1996). Especially, an increase in mortality at potential ages and sizes at maturation is expected to select for an earlier onset of maturation (Charlesworth 1994; Taborsky et al. 2003; Ernande et al. 2004). Specifically, it has been hypothesized that the collapse of the Canadian cod populations was a major selective episode strongly favouring early-maturing genotypes relative to late-maturing genotypes (Hutchings 1999).

Yet, detecting contemporary evolution in the wild is a major challenge. It requires that genetic changes are successfully identified among the total phenotypic variation. Expressed life history traits will be influenced not only by genetics but also by environmental variation through phenotypic plasticity. Harvested fish populations typically show trends towards an increased percentage of mature individuals at younger ages and smaller sizes, the Canadian cod populations being no exception (Trippel 1995). While these changes could reflect genetic responses to fishing mortality (Law and Grey 1989; Heino 1998; Heino and Godø 2002), they may also result, through phenotypic plasticity, from increased resource availability and faster growth of survivors after stock biomass has been depleted. Faster-growing individuals will often mature at an earlier age than slower-growing individuals (Alm 1959). Because of such confounding effects, the nature of phenotypic changes in exploited fish populations is not yet well understood (Law 2000).

Maturation reaction norms can shed new light on the relative roles of environmental fluctuations and genetic changes as causes of variation in maturation patterns (Heino et al. 2002*a*). By definition, a reaction norm describes the phenotypes expressed by a genotype under different environmental conditions (Schmalhausen 1949). Stearns and Koella (1986) used variation in somatic growth as a surrogate for variation in environmental conditions when modeling reaction norms for age and size at maturation. A recently developed probabilistic extension of this reaction norm approach (Heino et al. 2002*a*) models the maturation process based on the probability that individuals having reached a given age and size mature in the next season. By construction, this probability is independent of variations in growth and survival that determine the likelihood that individuals reach a given age and size (Heino et al. 2002*a*). Hence, the probabilistic reaction norm approach is useful for detecting changes in maturation, without being confounded by changes in growth and survival, and can thereby help to disentangle the effects of phenotypic plasticity and of genetic variation on maturation (see Materials and methods: Maturation reaction norms). The probabilistic maturation reaction norm terminology assumes that variation in growth is mainly environmentally determined (see Discussion).

For management purposes, it is important to be able to detect changes in life histories in exploited populations as early as possible. There are several reasons for this need. First, rapid evolutionary life history responses caused by experimental harvesting that mimics fishing (removal of larger individuals) have been shown to cause a significant reduction in harvestable biomass (Conover and Munch 2002). Second, in Atlantic cod and in many other species of fish, young females are known to breed for a shorter period, produce fewer egg batches, exhibit lower fecundity, and produce smaller eggs with lower fertilization and hatching rates compared with older spawners (Trippel 1998; Berkeley et al. 2004*a*). Third, it is important to understand the underlying causes of changes in life histories, in particular, whether these are mainly due to phenotypic plasticity or genetics. While plastic changes are in principle easily reversible, this may not be the case for genetic changes. Fourth, detecting life history changes at an early stage may aid managers by providing important additional clues about the status of a population. While population size is often the variable of focal interest for managers, it can be very difficult to detect changes in the abundance of populations in the wild. In oceanic fish populations, uncertainties in harvest statistics are typically large, and the same applies to population abundance surveys (Trippel 1995; Myers et al. 1997). An observed shift toward earlier maturation could then serve as a "stress" indicator (Trippel 1995).

In this study, we employ the new method of estimating probabilistic reaction norms for age and size at maturation of Atlantic cod populations found off Labrador and Newfoundland in the Northwest Atlantic. We characterize the maturation process in the years prior to, during, and after the dramatic collapse of these populations in the late 1980s and early 1990s, independently of temporal changes in growth and survival rates, and thereby provide new insights about the biology of these stocks as well as about the relative roles of environmental fluctuations and genetic changes as causes of changing maturation patterns. Previously, we have estimated maturation reaction norms for female cod from off southern Labrador and eastern Newfoundland (Olsen et al. 2004), finding evidence for maturation reaction norms having shifted toward earlier ages and smaller sizes during the stock collapse, which strongly suggests that an evolutionary response to high fishing pressure took place in this period. Here, we expand on these findings by comparing the maturation reaction norms of both female and male cod sampled from a broader geographic area. We also discuss how reaction norms for age and size at maturation may serve as biological indicators, or reference points, for the management of harvested populations.

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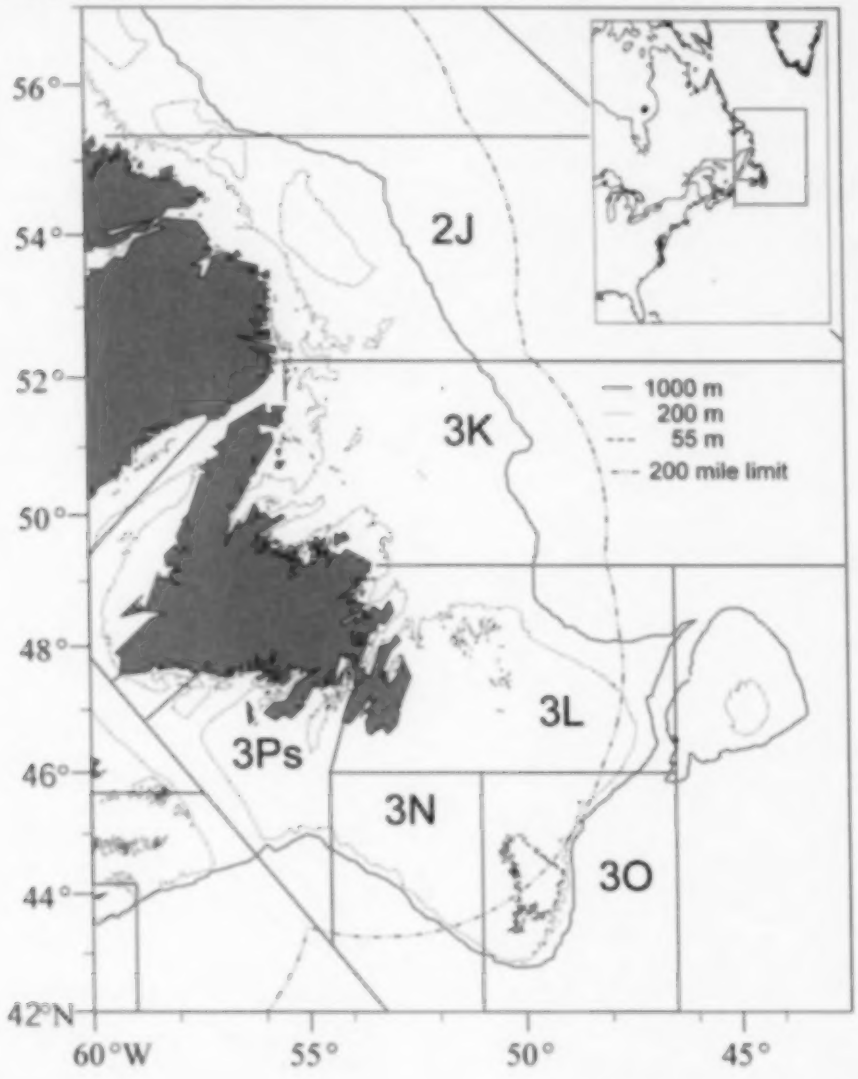
Fig. 1. Study area off the coast of Labrador and Newfoundland in eastern Canada (inset) showing physiographic features and Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps.



Materials and methods

Northern (2J3KL) cod

The designation "northern cod" refers to Atlantic cod found off southern Labrador (Northwest Atlantic Fisheries Organization (NAFO) Division 2J) through the Northeast Newfoundland Shelf (Division 3K) to the northern half of the Grand Bank off eastern Newfoundland (Division 3L) (Fig. 1). Northern cod is probably structured into several (sub)populations (Templeman 1966; Ruzzante et al. 1998; Beacham et al. 2002).

The collapse in the late 1980s and early 1990s reduced the cod abundance to about 2% of that in the early 1980s (Taggart et al. 1994; Myers et al. 1997; Lilly et al. 2003). There has been much controversy about the relative importance of fishing mortality, natural mortality, and emigration as causes of the collapse. Some argue that fishing was by far the most important driving factor (Hutchings and Myers 1994; Hutchings 1996; Myers et al. 1996). Others suggest that a spectrum of environmental factors, both abiotic and biotic, changed during the period of stock collapse; these factors may have increased the natural mortality of cod as well as induced shifts in its geographical distribution (Baird et al. 1992; deYoung and Rose 1993; Kulka et al. 1995). Still, there is broad agreement that increased fishing mortality was an important factor in the collapse (Rose et al. 2000; Smedbol et al. 2002).

In July 1992, the Canadian government declared a moratorium on directed fishing of northern cod. This moratorium has remained in effect in the offshore but was lifted for a few years (1998–2002) to allow a small fishery in the inshore (Lilly et al. 2003). Despite the moratorium, northern

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cod has not recovered, and its estimated population biomass remains at a historically low level (Lilly et al. 2003). There are several hypotheses as to why northern cod has not recovered; these include bycatches in fisheries directed at other species (Lilly et al. 2003), poor food availability (Rose and O'Driscoll 2002), increased predation from harp seals (Bundy 2001), various Allee effects (Frank and Brickman 2000; De Roos and Persson 2002; Rowe and Hutchings 2003), predation by other fish on cod eggs, larvae, and very early juveniles (Swain and Sinclair 2000; Walters and Kitchell 2001), and reductions in the reproductive potential of the spawning fish (Trippel 1995; Anderson and Rose 2001). The last hypothesis is inspired by the low number of spawning individuals and the truncated age distribution now characterizing the northern cod populations (Lilly et al. 2003).

Southern Grand Bank (3NO) cod

Cod in NAFO Divisions 3NO inhabit the southern Grand Bank of Newfoundland (Fig. 1). Like northern cod, the 3NO cod populations suffered a major decline in biomass in the late 1980s and early 1990s (Myers et al. 1997; Healey et al. 2003). The population structure of 3NO cod is not rigorously defined, and some seasonal mixing with cod in Subdivision 3Ps may occur (Healey et al. 2003). A moratorium on directed fishing of 3NO cod was imposed in February 1994 and has remained in effect since. Despite this effort, 3NO cod also has not recovered (Healey et al. 2003). It is suggested that bycatch of cod in other fisheries has increased to a point where it is impeding stock recovery (Healey et al. 2003).

St. Pierre Bank (3Ps) cod

Cod in NAFO Subdivision 3Ps is found south of Newfoundland on and around the St. Pierre Bank (Fig. 1). The population structure of 3Ps cod is not well defined, and the stock is considered a complex mixture of subcomponents. The abundance of 3Ps cod decreased substantially in the late 1980s and early 1990s, although the collapse was not as dramatic as for northern cod or for southern Grand Bank cod (Myers et al. 1997; Lilly et al. 2003). The 3Ps cod stock was under a moratorium from August 1993 to 1997, and population sizes have, in marked contrast with northern cod and southern Grand Bank cod, rebuilt to a considerable extent since the collapse (Brattey et al. 2003).

Analyzed data

We analyzed data on Atlantic cod caught in stratified random bottom-trawl surveys conducted annually by the Canadian Department of Fisheries and Oceans. Autumn surveys cover the distribution range of northern cod (2J3KL), while the data on cod from the southern Grand Bank (3NO) and the St. Pierre Bank (3Ps) are mainly from spring surveys. There is also a spring survey on northern cod from Division 3L. The autumn surveys are normally conducted during October to November and the spring surveys usually during April to May. The autumn survey was initiated in Divisions 2J and 3K in 1977 and in Division 3L in 1981. The spring survey was initiated in Divisions 3L, 3N, and 3O in 1971 and in Division 3Ps in 1972. Age and maturity sampling of captured cod was stratified by fish body length (Shelton et al. 1999; Lilly et al. 2003). Cod were aged on the basis of otoliths that contain annual rings reflecting a fish's seasonal growth pattern (Rollefsen 1933). Sex and maturity status were determined by visual inspection of the gonads. Body length was measured to the nearest centimetre. Age is here expressed as if the cod were sampled on their nominal birthday (1 January), which required adding 1 year to the ages from the autumn survey. Further details about sampling procedures and data are given in Lilly et al. (2003), Brattey et al. (2003), and Healey et al. (2003).

All cod of age 1 and 2 years were juvenile and were not included in the analyses. These youngest age-classes were also poorly represented in the samples owing to the sampling device used (Lilly et al. 2003). Note that the Engel trawl used for sampling the cod was changed in 1995, and the new Campelen trawl is more effective at catching the smallest cod (Lilly et al. 2003).

For 2J3KL cod, sample sizes of fish aged 7 years and older dropped to very low levels in the early 1990s (Lilly et al. 2003); robust estimates of the parameters describing growth and maturation at these ages could therefore not be obtained. Accordingly, analyses of maturation patterns were performed on 3- to 6-year-old fish. Most males in 2J3KL are mature at age 7, and most females in 2J3KL are mature at age 8 (Lilly et al. 2003). For 3NO and 3Ps cod, analyses were performed on 3- to 8-year-old fish. The statistical analyses were based on a total sample of 57 532 fish (Table 1).

The spring data from Division 3L were included mainly for comparison with the autumn survey in this area. This comparison will determine if sampling fish in the fall, several months before spawning, has an impact on the results. The cod considered in this study spawn mainly during a 3- to 4-month period in late winter and spring (Hutchings and Myers 1993; Myers et al. 1993), and it is possible that recruit spawners could develop gonads over the winter. Unless otherwise specified, Division 3L will hereafter refer to the autumn survey.

Maturation reaction norms

The probabilistic reaction norm for age and size at maturation is defined by the age- and size-specific probabilities with which an immature individual matures during a given time interval (Heino et al. 2002*a*). A description of the entire reaction norm involves specifying these probabilities for all relevant ages and sizes. For many purposes, it will be convenient to plot only the reaction norm midpoints, i.e., those combinations of age and size for which the estimated probability of maturing is 50%.

Maturation reaction norms should not be confused with other quantities, known as maturity ogives, traditionally used for describing a population's maturation status by estimating the proportion of mature individuals at a given age. The development of methods for estimating probabilistic maturation reaction norms was motivated by realizing that maturity ogives depend not only on the inherent maturation tendency of individuals (which is genetically coded) but also on the prevailing conditions for growth and survival (which affect the ogives both directly and through phenotypic plasticity). By contrast, the probabilistic reaction norm approach overcomes the potential confounding effects of growth and mortality, by estimating maturation probabilities conditional on individuals having reached a certain age and size. Variation

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Table 1. Sample sizes for surveys of Atlantic cod (*Gadus morhua*) conducted annually by the Canadian Department of Fisheries and Oceans in Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps.

Division	Survey	Years	Ages (years)	Females	Males	Total
2J	Autumn	1977–2002	3–6	3 711	3 773	7 484
3K	Autumn	1977–2002	3–6	4 667	4 364	9 031
3L	Autumn	1981–2002	3–6	3 133	3 131	6 264
3L	Spring	1971–2002	3–6	4 077	3 962	8 039
3NO	Spring	1971–2002	3–8	6 822	6 764	13 586
3Ps	Spring	1972–2002	3–8	6 958	6 170	13 128
Total				29 368	28 164	57 532

Note: No data exist for spring 1974 in Subdivision 3Ps, spring 1983 in 3NO, and autumn 1984 in 3L.

in growth will thus only influence which parts of a reaction norm can be observed but is expected to leave the position of the reaction norm unchanged. A consistent shift in the position of the reaction norm itself is thus strongly indicative of an evolutionary change in maturation (Stearns and Koella 1986; Heino et al. 2002*a*). This view assumes that maturation reaction norms are under genetic control and may evolve in response to selection pressures (Via and Lande 1985; Stearns and Koella 1986). There is evidence for genetic variation in reaction norms in fishes, both for early life history traits (Haugen and Vøllestad 2000) and for sexual maturation (McKenzie et al. 1983).

The data available for this study do not distinguish between first-time and repeat spawners. To estimate the probability of maturing, we used a refinement of the probabilistic reaction norm method (Barot et al. 2004*a*) by which the probability of maturing at age a and size s, denoted by $m(a,s)$, is derived from the probability of being mature at age a and size s, denoted by $o(a, s)$, and from the mean annual growth increment at age a, $s(a)$:

$$(1) \qquad m(a, s) = [o(a, s) - o(a - 1, s - \Delta s(a))]/[1 - o(a - 1, s - \Delta s(a))]$$

where $\Delta s(a)$ refers to the length gained from age $a - 1$ to age a. The function $o(a, s)$ is referred to as the age- and size-based maturity ogive. The above equation for $m(a, s)$ determines the probability of maturing as the frequency of fish that have matured (numerator) relative to the frequency of fish that could have matured (denominator). The equation is exact only when immature and mature individuals within a given age- and size-class have the same survival and growth rates. As demonstrated by Barot et al. (2004*a*), this estimation is relatively robust to a relaxation of this assumption.

Estimating maturation probabilities thus involves four steps: (*i*) estimation of maturity ogives, (*ii*) estimation of growth rates, (*iii*) estimation of the probabilities of maturing, and (*iv*) estimation of confidence intervals around the obtained maturation probabilities. Maturity ogives were estimated by fitting logistic regression models to the data (Collett 2003), with individual maturity state (juvenile or mature) as a binary response variable. We carried out separate analyses for each sex and NAFO Division (Divisions 3N and 3O were pooled to accommodate for their small samples sizes). We were not able to analyze the full interaction between cohort, age, and body length while using cohort and age as factors. Barot et al. (2004*a*) showed that such a full model requires sample sizes of about 100 individuals per cohort and age-class to obtain robust estimates. Therefore, our ogive model had to be simplified. By inspecting parameter estimates and their errors, and through standard model selection (Collett 2003) based on different candidate models, we decided to model age as a variate (linear effect) while keeping cohort as a factor; also, the interaction effect between cohort and age could be retained in the model

$$(2) \qquad \text{logit}(o) = \beta_0 + \beta_1 \cdot \text{length} + \beta_{2,c} + \beta_3 \cdot \text{age} + \beta_{4,c} \cdot \text{age}$$

where c denotes cohort. The cohort × age interaction (fifth term) is needed for detecting age-dependent temporal changes in the probability of being mature. Growth was estimated as the difference in mean body length between two consecutive ages of a cohort. Reaction norm midpoints were estimated by fitting logistic regression models to the reaction norm estimates, $m(a, s)$, independently for each age and cohort

$$(3) \qquad \text{logit}(m) = \beta_0 + \beta_1 \cdot \text{length}$$

and substituting 0.5 for m (Barot et al. 2004*a*).

As described above, probabilities of maturing are obtained through a sequence of statistical analyses. Since confidence intervals for the reaction norm parameters thus cannot be obtained directly, bootstrap techniques are used instead (Manly 1997). A bootstrapped sample was constructed for each cohort and age, where individuals are chosen at random with replacement from the original data set. The resampling was repeated 1000 times. We fitted linear regression models to the reaction norm midpoints to test for temporal trends in maturation. Confidence intervals around the regression parameters were derived from the 1000 bootstrap replicates, with the 2.5 and 97.5 percentiles being set as lower and upper confidence limits, respectively. All analyses were performed without weighting the observations by population abundance at length (Morgan and Hoenig 1997; Barot et al. 2004*a*), since preliminary analyses revealed that such weighting did not affect the conclusions about the data but tended to introduce more noise in the model estimates.

Survival and age at 50% maturity

Mainly for descriptive purposes, we present estimates of annual survival rates and of the traditional ogive-based measure of maturation, the age at 50% maturity. Annual survival

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probabilities $S_{a,y}$ at age a in year y were estimated from survey catch data as

$$(4) \qquad S_{a,y} = C_{a,y}/C_{a-1,y-1}$$

where $C_{a,y}$ is the catch abundance per unit effort at age a in year y (Brattey et al. 2003; Healey et al. 2003; Lilly et al. 2003). The change in survey gear that took place in 1995 (Engel trawl replaced with Campelen trawl) could potentially have influenced trends in survival; hence, the Engel data have been transformed to Campelen equivalents (for details, see Lilly et al. 2003). These Campelen equivalents were available for the years 1983–1994. Age at 50% maturity was estimated from logistic regression models with year as a factor and age as a variate:

$$(5) \qquad \text{logit}(o) = \beta_0 + \beta_1 \cdot \text{age} + \beta_{2,y} + \beta_{3,y} \cdot \text{age}$$

Results

Survival, growth, and age at 50% maturity

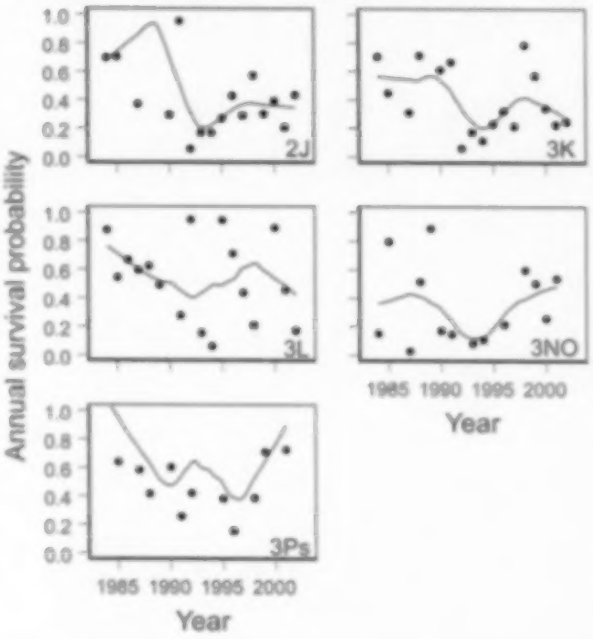
The estimates of annual survival probabilities are relatively noisy, but very low values are found in the early 1990s (Fig. 2). The estimates are generally higher again during the moratorium years (Fig. 2). Annual length increments, averaged for 4- to 6-year-old cod, lie between 4 and 12 cm·year^{-1} (Fig. 3). The growth estimates are lower in the north (Divisions 2J and 3K) compared with the south (Divisions 3NO and 3Ps) (Fig. 3). There are no clear temporal trends in growth rates, but the lowest estimates are found in the early to mid-1990s (Fig. 3). In Divisions 2J, 3K, and 3L, the age at 50% maturity in females decreased from about 6 years in the 1980s to about 5 years in the mid-1990s (Fig. 4). In Divisions 3NO and 3Ps, the age at 50% maturity in females varied between 5.5 and 7 years in the 1970s and 1980s and decreased to about 4.5–5.5 years in the 1990s (Fig. 4). Male age at 50% maturity is about 1 year below female age at 50% maturity and shows a similar trend over time (Fig. 4). Our analyses agree with results that have been reported earlier in terms of instantaneous total mortalities, mean body length at age, and maturity ogives (Brattey et al. 2003; Healey et al. 2003; Lilly et al. 2003).

Maturation reaction norms

We were able to estimate maturation reaction norms for two or three ages for a given sex and division. For younger or older fish outside such an age bracket, data were either too sparse or too skewed towards juvenile or mature individuals. As an example, we show the reaction norms for female and male cod of the 1980 cohort in Division 3Ps. These reaction norms had negative slopes, meaning that the body length at which the cod reach a given maturation probability decreases with age (Fig. 5). Furthermore, the male reaction norms were positioned below the female reaction norms (Fig. 5), implying that for a given age and body length, a male has a higher maturation probability than a female. These patterns were qualitatively similar for most other cohorts for which reaction norms could be estimated (additional reaction norms are not shown but can be derived from Figs. 6 and 7).

Maturation patterns varied throughout the survey period. Most notably, there is a consistent temporal trend in all five

Fig. 2. Mean annual survival rates of 4- to 6-year-old Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps fitted with a locally weighted regression smoother. The smoothing parameter (span) is set to 0.5. Point estimates exceeding 1 are not shown but were included when fitting the regression.



geographic areas (2J, 3K, 3L, 3NO, and 3Ps) and for both males and females: reaction norm midpoints (i.e., age-specific body lengths resulting in a 50% probability of maturing) decline by about 15–25 cm through the 1980s and early 1990s (Figs. 6 and 7; Table 2). This decline in reaction norm midpoints means that maturation at a given growth rate shifted toward earlier ages and smaller body lengths. Furthermore, there appears to be a moment in time, around 1993–1995, from which onwards there is no further decrease in reaction norm midpoints (Figs. 6 and 7; Table 2). We used the year in which each moratorium was introduced as a logical break point for analyzing these finer patterns in the data. For the period subsequent to the start of each moratorium, there is evidence for differences among the sexes in the trends in reaction norm midpoints. The females show a significantly positive slope in all geographic areas, although not always at age 6 years, owing to sparse data at that age (Table 2). Males show a significantly positive slope only in Divisions 3K and 3L, and their slopes are generally not as steep as for the females in the same areas (Table 2).

Together, Figs. 5–7 suggest that (independent of differences in growth and survival) males tend to mature at smaller body sizes and younger ages compared with females and that there is a spatial trend by which maturation probabilities increase with latitude for all ages and sizes. These patterns are best seen by comparing smoothed temporal trends in reaction norm midpoints at age 5 years for all divisions (Fig. 8).

Notice that changes in the observed sizes and maturity frequencies at each age occurring over winter could, in prin-

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Fig. 3. Mean annual length increments of 4- to 6-year-old Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps fitted with a locally weighted regression smoother. The smoothing parameter (span) is set to 0.5.

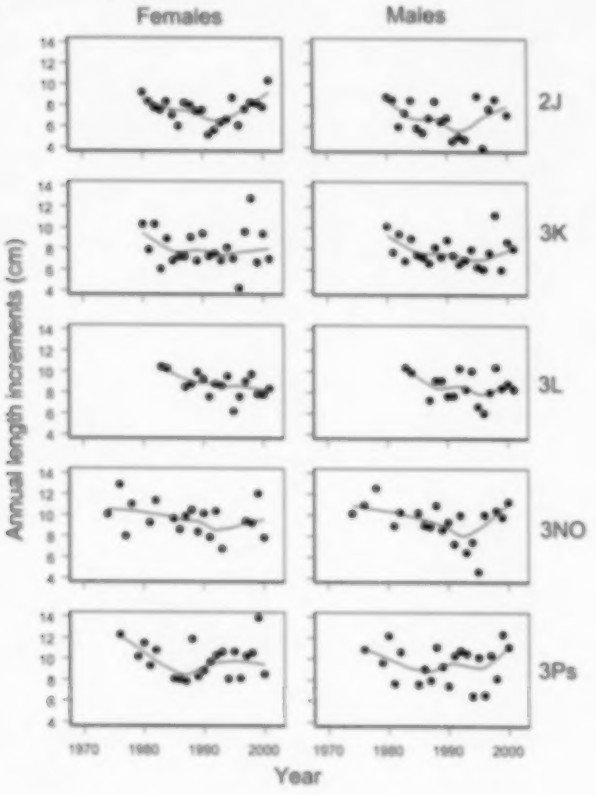
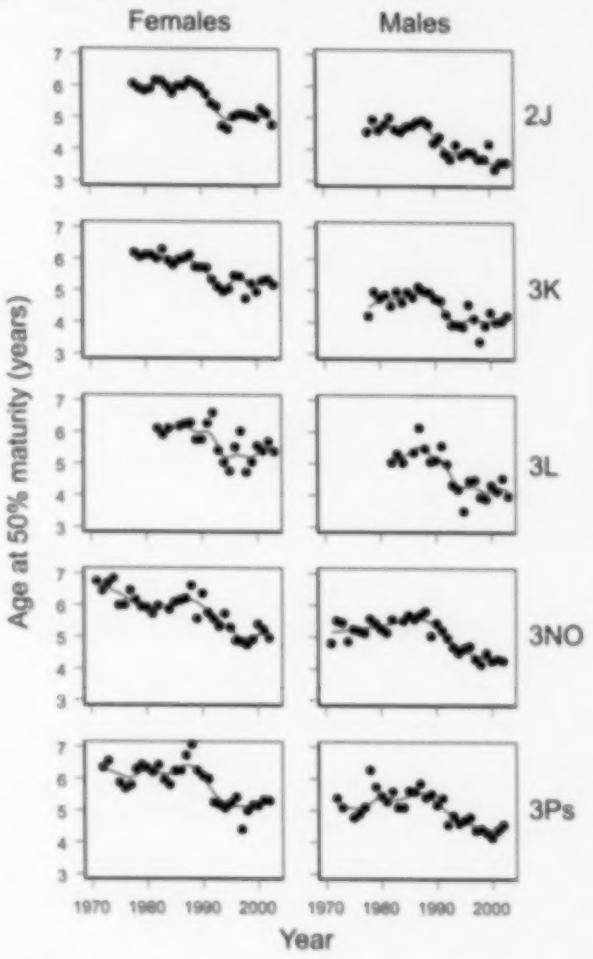


Fig. 4. Ages at 50% maturity of Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps fitted with a locally weighted regression smoother. The smoothing parameter (span) is set to 0.3.



ciple, induce differences in reaction norm midpoints estimated from autumn versus spring surveys. Reassuringly, for Division 3L, for which we have data from both autumn and spring, this appears not to be the case: the estimated reaction norm midpoints are very similar (Fig. 9). Temporal overlap between the two surveys in 3L is reduced because, owing to the scarcity of data, reaction norm midpoints could not be estimated from spring data from about 1990 onwards.

From a management perspective, the following question is of high relevance: at what moment in time could the decline in reaction norm midpoints have been detected? We have explored this question by going back in time (in steps of 1 year from the year in which the moratorium was introduced), computing reaction norm midpoints and slopes from the restricted data that were available to managers at that time. We limited this analysis to 6-year-old females, as these exhibited relatively precise estimates for the period up to the moratorium. This retrospective analysis indicates that the negative slopes in reaction norm midpoints could have been detected in all areas by 1990. In some divisions, these trends could have been picked up even earlier: negative slopes could have been detected in the early 1980s in 3Ps, in the mid-1980s in 2J, 3K, and 3NO, and around 1990 in 3L (Fig. 10).

Discussion

This study provides evidence for contemporary life history evolution in one of the world's leading food fish, the Atlantic cod. We show that the maturation schedule of Atlantic cod off southern Labrador and Newfoundland shifted towards earlier ages and smaller body sizes in the 1980s and early 1990s. This shift is demonstrated through changes in the reaction norm for age and size at maturation and thus is not confounded by concomitant changes in growth or survival. The same trend was shown independently for both female and male cod from five neighbouring geographic areas (NAFO Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps). Our findings strongly suggest that the collapse of the cod populations off southern Labrador and Newfoundland, which took place during the late 1980s and the early 1990s, was a distinct selective episode that favoured early-maturing

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Fig. 5. Maturation reaction norms of (*a*) male and (*b*) female Atlantic cod (*Gadus morhua*) of the 1980 cohort from Northwest Atlantic Fisheries Organization (NAFO) Subdivision 3Ps shown in terms of body lengths at which the probability of maturing equals 25%, 50% (reaction norm midpoint), and 75% (solid lines). Growth rates are depicted as arithmetic mean length at age (shaded lines) together with 5th and 95th percentiles (broken shaded lines).

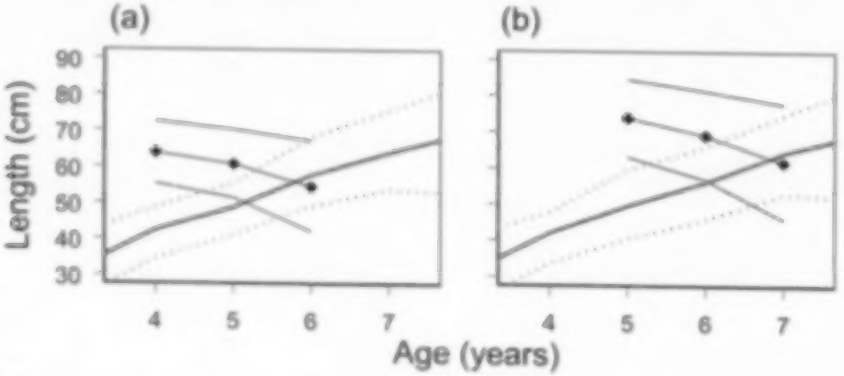

Fig. 6. Temporal trends in maturation reaction norm midpoints of female Atlantic cod (*Gadus morhua*) at ages 5 and 6 years from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps. Some cohorts are missing owing to insufficient data.

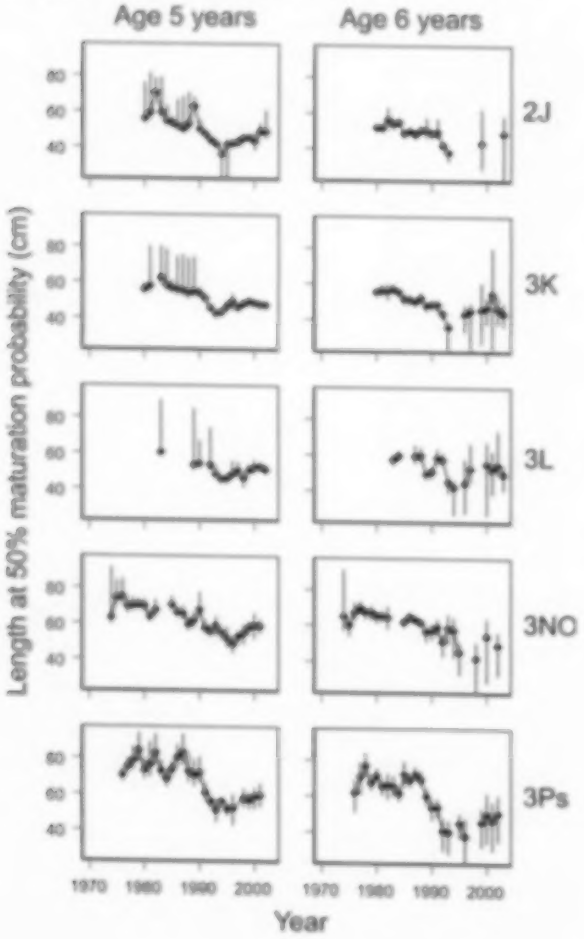

Fig. 7. Temporal trends in maturation reaction norm midpoints of male Atlantic cod (*Gadus morhua*) at ages 4 and 5 years from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps. Some cohorts are missing owing to insufficient data.

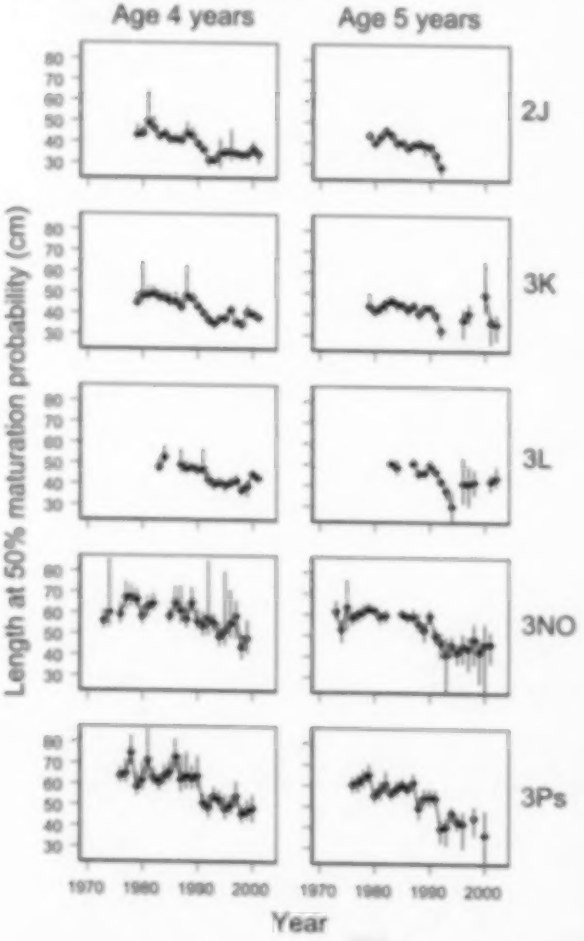

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Table 2. Temporal trends in maturation reaction norm midpoints in Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps.

Division	Age (years)	Regression slope, cm·year^{-1} (95% confidence interval)	
		Premoratorium	Moratorium
Female			
2J	5	−1.15 (−2.19, −0.87)	1.06 (0.68, 2.33)
2J	6	−0.67 (−0.99, −0.37)	—[a]
3K	5	−0.82 (−1.88, −0.50)	0.51 (0.26, 0.79)
3K	6	−0.97 (−1.23, −0.75)	1.00 (−0.24, 2.29)
3L	5	−0.84 (−3.36, 0.88)	0.63 (0.25, 1.03)
3L	6	−0.39 (−1.04, 0.07)	0.98 (0.16, 2.74)
3NO	5	−0.71 (−1.18, −0.56)	1.69 (0.63, 2.66)
3NO	6	−0.55 (−1.15, −0.40)	0.99 (−3.89, 11.55)
3Ps	5	−1.05 (−1.33, −0.78)	0.90 (0.19, 1.89)
3Ps	6	−1.34 (−1.68, −1.01)	1.25 (−0.84, 3.00)
Male			
2J	4	−0.80 (−1.20, −0.62)	0.25 (−0.50, 0.72)
2J	5	−0.82 (−1.07, −0.69)	—[a]
3K	4	−0.61 (−1.08, −0.43)	0.30 (0.057, 0.53)
3K	5	−0.49 (−0.73, −0.33)	−0.17 (−1.63, 1.07)
3L	4	−0.69 (−1.16, −0.12)	0.33 (0.04, 0.62)
3L	5	−0.60 (−1.19, −0.47)	1.02 (0.39, 2.13)
3NO	4	−0.38 (−0.70, −0.053)	−1.83 (−10.78, 0.23)
3NO	5	−0.65 (−1.31, −0.52)	0.43 (−3.12, 1.92)
3Ps	4	−0.70 (−0.96, −0.46)	−0.63 (−1.69, 0.36)
3Ps	5	−0.99 (−1.23, −0.81)	−1.24 (−4.57, 0.63)

Note: Regressions are shown for premoratorium years (including the year in which each moratorium was declared) as well as for subsequent years. The moratorium was initiated in July 1992 in Divisions 2J, 3K, and 3L, in February 1994 in Divisions 3NO, and in August 1993 in Subdivision 3Ps. The moratorium was lifted in 1997 in 3Ps; this is not taken into account in the analyses.

[a]Not estimable owing to sparse data.

genotypes relative to late-maturing genotypes. This conclusion is in agreement with earlier findings based on a subset of the data analyzed here (female northern 2J3KL cod; Olsen et al. 2004).

We note that age and size will typically not explain all variation in maturation, so that trends in the reaction norms could still be influenced by hypothetical trends in phenotypically plastic responses that are unrelated to growth, age, or size. First, a cod in good condition will likely have a higher probability of maturing than a similarly sized and aged cod in poor condition (Marteinsdottir and Begg 2002). Cod off southern Labrador and eastern Newfoundland (Divisions 2J3KL) experienced a decrease in body condition during the period of collapse, except for fish in parts of Division 3L (Bishop and Baird 1994; Krohn et al. 1997). The net effect of this would be to delay maturation, contrary to observations. It is not likely, therefore, that trends in body condition have caused the trends in reaction norms reported here for these areas. Second, the estimated reaction norms could be influenced by the social environment experienced by the fish. For example, in the southern platyfish (*Xiphophorus maculatus*), the presence of dominant males has been shown to suppress maturation of subordinate males (Sohn 1977). Since social suppression of subordinate, and likely smaller, adults would be released during a period of catastrophic population decline, this effect could account for some of the observed changes in reaction norms. Third, there could be a residual effect of temperature on the maturation reaction norms. For North Sea plaice (*Pleuronectes platessa*), it has been shown that the probability of maturing at a given age and length increased significantly with increased temperature 2 and 3 years prior to maturation (Grift et al. 2003). However, the collapse of the cod populations off Labrador and Newfoundland coincided with a prolonged period of low water temperatures (Drinkwater 2002). The net effect of this, as suggested by the study of North Sea plaice, would be to displace the reaction norms toward older ages and larger sizes, while the opposite was in fact observed.

We also wish to highlight a semantic issue that sometimes leads to confusion. The term maturation reaction norm implies, through its historical usage in the literature, that the variation of age and size at maturation along the reaction norm is mostly a phenotypically plastic response, in this case to variation in growth. Our usage of this term thus implies that variation along the reaction norm is mostly caused by environmental, as opposed to genetic, factors. While it is known that genetic variability in growth exists and that growth rates may thus evolve as a response to selective harvesting (Conover and Munch 2002; also see Sinclair et al. 2002; Munch et al. 2005), it is very unlikely that growth variation in a species exposed to an environment as unpredictable as that of Atlantic cod is primarily genetic. Even if this were different (perhaps for another species), the valuable descriptive properties of these reaction norms do not depend on their naming and thus not on the actual origin of growth variation. In the longer run, future research may aim to determine whether, and, if so, how, maturation evolution and growth evolution are interacting, both ecologically and genetically.

We found that the age-specific body length at which maturation probability reaches 50%, referred to as the reaction norm midpoint in this study, was smaller for male cod as compared with female cod. This implies that, for a given growth rate, male cod will tend to mature at earlier ages and smaller body sizes. This sex difference in maturation pattern conforms well to results based on the more traditional method of maturity ogives (Morgan 2000; Brattey et al. 2003), considering that there seems to be no major sex difference in growth. Also, the fact that females show a more pronounced reversal of maturation patterns during the moratorium years supports the suggestion that selection pressures have differed, and continue to differ, between the sexes. For female cod, a large body size offers an indisputable fitness advantage, in terms of both increased fecundity and improved offspring quality (Trippel 1998). For male cod, on the other hand, the benefits of large body size are less obvious. Tank experiments in which female cod had access to both small and large males revealed no positive association between male body size and reproductive success; in fact, many of the smaller males exhibited a higher success than their larger-sized competitors (Rakitin et al. 2001).

Our data indicate that from about 1993 to 1995, after the closing of the fisheries, the trends in the maturation norms are halted and, for females, even show signs of reversal. To

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Fig. 8. Maturation reaction norm midpoints at age 5 years for (*a*) female and (*b*) male Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J (dashed line), 3K (dotted line), 3L (solid line), and 3NO (shaded line) and Subdivision 3Ps (dashed shaded line) fitted with a locally weighted regression smoother. The smoothing parameter (span) is set to 0.4. The arrows indicate how the maturation reaction norms are ordered with respect to increasing latitude.

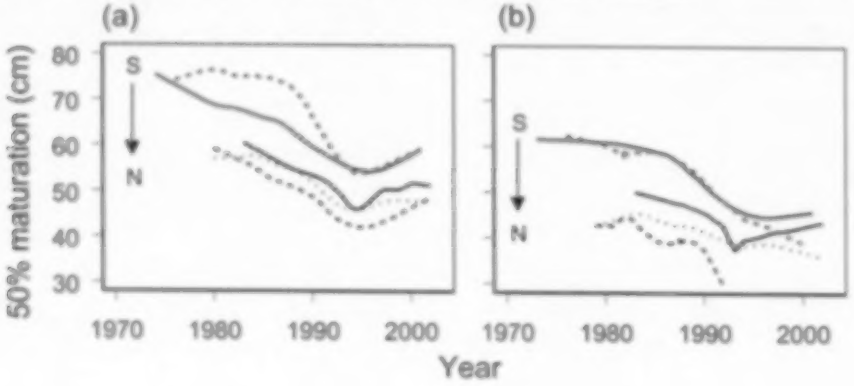
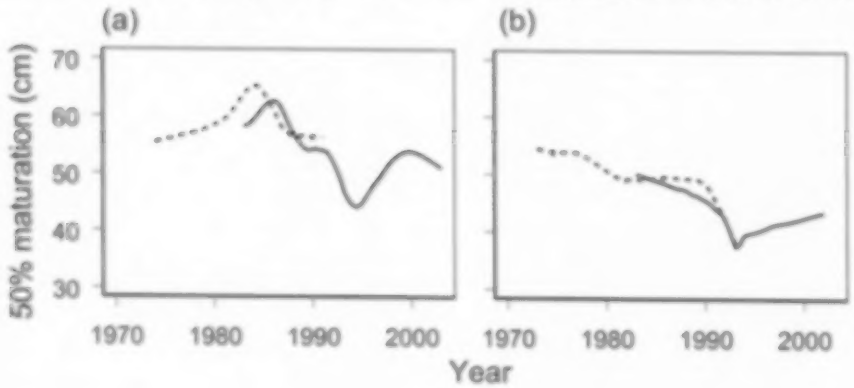


Fig. 9. Maturation reaction norm midpoints for (*a*) females at age 6 years and (*b*) males at age 5 years of Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Division 3L based on spring survey data (broken line) and autumn survey data (solid line) fitted with a locally weighted regression smoother. The smoothing parameter (span) was set to 0.4.



some extent, the signs of reversal are a surprising result because, in theory, genetic change caused by fishing will not be easily reversed: selection for early maturation appears to be much easier, and faster, than for late maturation (Law and Grey 1989). Still, field experiments on freshwater fish have documented rapid evolution towards delayed maturation when predation pressure was relaxed (Reznick et al. 1990). It is possible that the fitness benefits of large size in female cod (as discussed above) are stronger than until now considered in models. Also, it is possible, in theory, that immigration of genotypes with different maturation schedules could have influenced the recent trends in maturation reaction norms. Importantly, the period since initiation of the moratoria has been only a decade; to better understand whether the conjectured trend in maturation schedules is borne out, we shall have to await the results of future research surveys.

We also found evidence for a geographical trend by which the age-specific body length at 50% maturation probability decreased with increasing latitude (also see Morgan et al. 1994). This north–south gradient was substantial, and opposite to the effect of the latitudinal gradient in growth on the timing of maturation. We therefore suggest that our results reveal countergradient variation in maturation tendency (Conover and Schultz 1995): the capacity for early maturation (as determined by the cod's genetics) appears to be greatest in areas with the least opportunity for early maturation (as determined by the phenotypically plastic consequences of differential growth). For instance, in the early 1980s, the reaction norm midpoints of 6-year-old females from off southern Newfoundland (Subdivision 3Ps) were around 70 cm as compared with only 50 cm for females from off southern Labrador. This finding suggests that genetic differences, consistent with the selective pressures of local adaptation, exist in the maturation schedules of cod from different parts of the Newfoundland–Labrador region. Tagging studies and population genetic studies corroborate that local population structure exists within this region (Templeman 1966; Ruzzante et al. 1998; Beacham et al. 2002). It thus seems likely that locally adapted life histories in Atlantic cod can evolve, despite the fact that cod is a highly mobile species inhabiting a marine environment without any obvious barriers to dispersal. As pointed out by Berkeley et al. (2004*b*)

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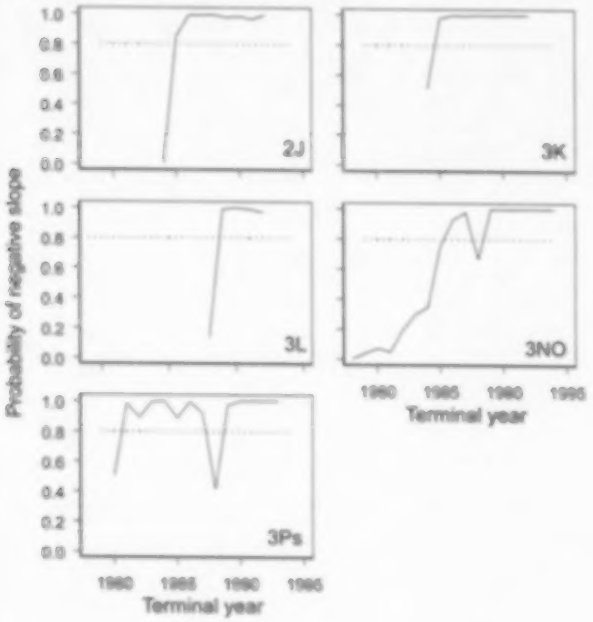
Fig. 10. Probability of a negative trend in reaction norm midpoints estimated for 6-year-old female Atlantic cod (*Gadus morhua*) when analysis is retrospectively restricted to only part of the available time series up to and including the given terminal year. The last terminal year shown corresponds to the year in which the moratorium was initiated. Broken lines show, for reference, the 80% level of the probability of a negative trend. The probabilities were calculated as the proportion of 1000 bootstrap replicates yielding a negative slope.



and Hutchings (2004), managers should thus take into account that marine exploited species may have a complex spatial population structure and life histories that are evolving on a contemporary time scale.

Maturation reaction norms have also been estimated for other heavily exploited populations of Atlantic cod, from Georges Bank as well as the Gulf of Maine (Barot et al. 2004*b*) in the northwest and from the Norwegian Sea as well as the Barents Sea (Heino et al. 2002*a*, 2002*b*, 2002*c*) in the northeast. Similar findings have been obtained for North Sea plaice (Grift et al. 2003; also see Rijnsdorp 1993) and American plaice (*Hippoglossoides platessoides*) (Barot et al. 2005). These studies provide evidence for adaptive changes in maturation schedules that point in the very same direction as those documented in this study of Labrador and Newfoundland cod.

We suggest that monitoring maturation reaction norms for age and size at maturation may aid decision making in the management of exploited marine resources in general and of Atlantic cod in the Newfoundland–Labrador region in particular. First, estimates of age- and length-specific maturation probabilities are needed to parameterize age- and length-structured population models (Frøysa et al. 2002) and hence provide important input for a broad spectrum of population assessment purposes. Second, information on trends in the maturation process may serve as a helpful warning signal with regard to changes in population size and recruitment potential. With the collapse of the cod populations off Labrador and Newfoundland in mind, Hutchings and Myers (1995) argued that the sustainability of any fishery clearly depends on quantifying a wide range of biological indicators of population health. Specifically, Trippel (1995) suggested that the age A_{50} at which 50% of fish are mature holds promise as one such stress indicator. We build on this argument and put forward maturation reaction norms as a biological indicator with important advantages over A_{50}. A reduction in A_{50} is ambiguous in that it may reflect either fisheries-induced selection favouring early maturation or maturation facilitated by faster individual growth in response to declining stock size. Both of these possibilities imply that fishing heavily impacts the population, which hence may be considered as being stressed. However, A_{50} may also decline if maturation is merely facilitated by a temperature increase or when the survival of mature fish increases. Neither of these scenarios represents a cause of concern for the management of a stock. By contrast, estimation of maturation reaction norms reveals changes in the maturation tendency itself, as shown here for the cod populations off Labrador and Newfoundland in the 1980s. A more robust indicator of population health may therefore be the length L_{P50} (Grift et al. 2003) at which the probability of maturing reaches 50% for a given age. The methodology described and utilized here enables estimation of L_{P50}.

In summary, this study shows that maturation of Labrador and Newfoundland cod shifted towards earlier ages and smaller body sizes during the severe collapse of these populations in the late 1980s and early 1990s. The use of reaction norm methodology removes confounding effects of growth or survival and thus provides stronger evidence for changes in the underlying maturation process than previous analyses could.

Acknowledgments

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Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*)[1]

Jeffrey A. Hutchings

Abstract: Changes to life history traits are often concomitant with prolonged periods of exploitation. In the Northwest Atlantic, 30- to 40-year declines of more than 90% of Atlantic cod (*Gadus morhua*) have been associated with significant reductions in age and length at maturity, changes most parsimoniously explained as genetic responses to fishing. Increased survival costs of reproduction associated with earlier maturity, resulting in higher natural mortality and shorter life span, negatively affect population growth rate and rate of recovery. Coupled with lower hatching rate among first-time spawners and smaller size at maturity, a modest reduction in age from 6 to 4 years can reduce annual population growth in Atlantic cod by 25%–30%, based on the output of a stochastic, age-structured life history model. Earlier maturity more than doubles the probability of negative population growth every generation. These results underscore the potential for fishing-induced changes to life history traits alone to generate slow or negligible recovery in marine fishes, exacerbating negative impacts on population growth resulting from ecosystem-level alterations to interspecific competition and predation.

Résumé : Des changements de caractéristiques démographiques accompagnent souvent les longues périodes d'exploitation. Dans le nord-ouest de l'Atlantique, les déclins sur 30 à 40 ans de l'ordre de plus de 90 % de la morue franche (*Gadus morhua*) sont associés à des réductions significatives de l'âge et de la longueur à la maturité, des changements qui s'expliquent, de la manière la plus parcimonieuse, comme étant des réactions génétiques à la pêche. Les coûts accrus de la survie à la reproduction associés à la maturité plus précoce, qui entraînent une mortalité naturelle plus élevée et une longévité réduite, affectent négativement le taux de croissance de la population et le taux de récupération. En conjonction avec un taux d'éclosion réduit chez les poissons qui fraient pour la première fois et une taille à la maturité plus faible, une réduction modeste de l'âge de 6 à 4 ans peut abaisser la croissance annuelle de la population de morues franches de 25–30 %, d'après les résultats d'un modèle démographique stochastique avec structure d'âge. Une maturité précoce plus que double la probabilité d'une croissance de population négative à chaque génération. Ces résultats soulignent que les changements de caractéristiques démographiques induits par la pêche peuvent produire une récupération faible ou négligeable chez les poissons marins, exacerbant ainsi les impacts négatifs sur la croissance de population qui résultent des modifications qui se font dans la compétition interspécifique et la prédation à l'échelle de l'écosystème.

[Traduit par la Rédaction]

Introduction

Exploitation affects life history. Changes to age and size at maturity, longevity, and quite possibly fecundity and egg size are the product of phenotypic and genetic responses to fishing (e.g., Rochet 1998; Law 2000; Hutchings 2002). Perhaps the most common phenotypic response is a reduction in age at maturity effected by faster rates of growth associated with reductions in population density (Policansky 1993). Hypothesized genetic responses to exploitation have also included changes to age and size at maturity, growth rate, and fecundity per unit body mass (Rijnsdorp 1993; Conover and Munch 2002; Grift et al. 2003). Phenotypic responses by a life history trait are a product of phenotypic plasticity, the precise nature of the response being reflected by an individual's (genotype's) norm of reaction for that trait, which describes how a phenotype responds to environmental change (Hutchings 2004). Genetic responses are the product of fishing activities that render some individuals, because of phenotypic differences in heritable traits such as body size and growth rate, more vulnerable to exploitation than others. The higher the rate of fishing mortality and the greater the number of generations over which a population has been fished, the greater the likelihood that genetic responses to

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J.A. Hutchings. Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada (e-mail: Jeff.Hutchings@Dal.ca).

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exploitation have occurred (Law 2000; Hard 2004). At the population level, one of the challenges in distinguishing phenotypic and genetic responses to fishing is the complication that fishing might differentially affect norms of reaction (Rijnsdorp 1993; Heino et al. 2002; Olsen et al. 2004). In other words, genetic responses are not restricted solely to changes in the average values of a trait but can also be reflected by changes to the ways in which individuals respond to environmental change (Haugen 2000; Hutchings 2004).

Phenotypic and genetic changes to life history traits are of interest to conservation biologists and resource managers because of the inextricable links that exist between these fitness-related characters and population growth rate. The former, manifested ultimately by age-specific schedules of survival and reproductive investment, are the primary determinants of individual fitness, usually represented either by r (intrinsic rate of increase) or by λ (finite rate of increase) (Roff 2002). The geometric mean of these individual fitness measures determines the growth rate of the population, r_{pop} and λ_{pop}, parameters positively associated with sustainable rates of harvesting, persistence, and rate of population recovery (Lande 1993; Myers et al. 1999).

The present study represents an exploratory analysis of the consequences of fishing-induced changes in life history to population growth in Atlantic cod (*Gadus morhua*), a species that has experienced precipitous declines throughout its geographical range. Since the early 1970s, North Sea cod have declined almost 90% (International Council for the Exploration of the Sea 2004); among stocks in the Northwest Atlantic, five have experienced even greater reductions, with declines over three-generation time intervals (roughly 30 years) as high as 99% (COSEWIC 2003) (Table 1). The reductions in population density concomitant with such declines are almost certainly sufficient to produce phenotypic change to life history traits. However, if fishing mortality during these declines was not random with respect to heritable phenotypic traits, one would expect some changes to life history to represent genetic responses to fishing. From a recovery perspective, empirical data across a broad spectrum of marine fishes have revealed that recovery by demersal species is significantly impaired by reductions in excess of 90% (Hutchings 2000).

I begin by describing changes to age and size at maturity concomitant with population decline for two of the most severely affected Northwest Atlantic cod stocks: Newfoundland and Labrador's northern cod and eastern Scotian Shelf cod. By examining prereproductive growth during periods of life history change, I am then able to evaluate the degree to which these changes can be explained solely as phenotypic responses to reductions in density. The influence of earlier maturity and smaller size at maturity on Atlantic cod population growth, and thus rate of recovery, is then assessed by a stochastic, age-structured life history model that allows survival costs of reproduction to increase with declining age at maturity (Beverton et al. 1994) and incorporates reduced hatching success among first-time spawners (Trippel 1998). This use of a stochastic model builds upon work pioneered by Lewontin and Cohen (1969), and extended by Roff (1974), who modelled the effects of random fluctuations in population growth rate on expectations of population size and probabilities of extinction.

Methods

Population growth rate

I used a stochastic, age-structured life history model previously developed by Hutchings (1999) to study the influence of changes to age and size at maturity on annual (r) and per-generation (R_0) rates of increase. Age-specific rates of survival and fecundity are used to estimate rates of population growth. These data are expressed as l_x, the probability of surviving from birth until the beginning of the breeding season at age x, and m_x, the number of eggs produced by a female breeding at age x. The intrinsic rate of population increase, r, can be calculated from the discrete-time version of the Euler–Lotka equation:

$$(1) \qquad 1 = \sum_{x=\alpha}^{x=\tau} l_x m_x \exp(-rx)$$

where α represents age at maturity and τ represents age at death ($\tau = 21$ years in the present analysis). Net reproductive rate, R_0, is given by

$$(2) \qquad R_0 = \sum_{x=\alpha}^{x=\tau} l_x m_x$$

Although probability distributions of the intrinsic rate of increase cannot be described by a stochastic model (because of the analytical constraint that r can only be calculated by iteration), r can be approximated by the natural logarithm of the net reproductive rate discounted by generation time (G) as $r = \ln(R_0)/G$, where $G = (\Sigma l_x m_x x)/(\Sigma l_x m_x)$. Probability distributions of R_0 were generated from 2000 randomizations per estimate using Microsoft® Excel. The highly positive skew of these distributions necessitated the calculation of r from median estimates of R_0. The population consequences of different life histories was summarized in terms of two model outputs: (*i*) an estimate of r (based on the median value of R_0, as determined from the simulations) and (*ii*) the expected probability of negative population growth (i.e., $\Pr(R_0 < 1)$).

The model contains both stochastic and deterministic elements, as described in more detail in the sections following. When estimating l_x, survival is partitioned into survival from birth to the beginning of age 3 (l_3), prereproductive survival ($l_{3-\alpha}$), and postreproductive survival ($l_{\alpha-\tau}$). Each of these is stochastic in the model. Age-specific fecundity (m_x) is a function of body weight, the proportional increase in body weight from one year to the next, and the relationship between body weight and fecundity. Weight at age and proportional increases in weight are stochastic; the relationship between body weight and fecundity was incorporated into the model without error. The only deterministic elements to the model are age at maturity, age at death, the parameter that specifies the survival cost of reproduction, and weights at maturity for individuals maturing at 4 and 6 years.

Age-specific survival, l_x, and survival costs of reproduction

The basic model incorporated observed or estimated variation in survival from birth to age 3, l_3 (the age at which most Northwest Atlantic cod are first recruited to commercial fishing gear), instantaneous rate of prereproductive mor-

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Table 1. Estimated changes in the abundance of mature individuals for Atlantic cod (*Gadus morhua*) stocks partially or entirely under Canadian management.

Stock	NAFO division(s)	Data source	Population decline (%)	Years
Northern cod	2J3KL	VPA–survey	99	1968–2001
Southern Grand Bank	3NO	VPA	98	1968–2001
Cabot Strait	4Vn	VPA	95	1981–2000
Northern Gulf	3Pn4RS	VPA	93	1975–2002
Eastern Scotian Shelf	4VsW	Survey	92	1975–2002
Western Scotian Shelf	4X	VPA	78	1979–2002
Georges Bank	5Zj,m	VPA	70	1979–2002
St. Pierre Bank	3Ps	VPA	46	1968–2001
Southern Gulf	4T	VPA	23	1973–2002

Note: Stocks are delineated by Northwest Atlantic Fisheries Organization (NAFO) divisional boundaries. Decline estimates are those reported for the three-generation periods corresponding to each stock by COSEWIC (2003). Abundance estimates were based on either fisheries-independent surveys or virtual population analysis (VPA).

tality, M_{imm}, and mortality of mature, postreproductive individuals, M_{mat}. Distinguishing mortality prior to and following maturity acknowledges, and allows for the inclusion of, a survival cost of reproduction (Beverton et al. 1994; Roff 2002). Survival from birth to age 3 was quantified from abundance estimates of northern cod (Lilly et al. 2001) and from age-specific fecundities, as described below, such that survival from birth to age 3 in year t, $l_{3(t)}$, was assumed to be a function of the number, n, of 7- to 11-year-olds in year $t - 3$ multiplied by the average fecundity of those individuals such that

$$(3) \qquad l_{3(t)} = n_{3(t)} / \sum_{x=7}^{x=11} n_{x(t-3)} m_{x(t-3)}$$

Survival from birth to age 3 estimated in this manner for the 1962 through the 1988 year-classes of northern cod was weakly density dependent (see Myers et al. 1995) and averaged $1.13 \times 10^{-6} \pm 1.11 \times 10^{-6}$ (±SD). I assumed that variation in annual mortality attributable to factors unrelated to reproduction (e.g., predation) was best reflected by a beta distribution given as

$$(4) \qquad f(x) = \frac{(x/s)^{(\theta-1)}[1-(x/s)]^{(\beta-1)}}{\Gamma(\theta)\Gamma(\beta)/\Gamma(\theta+\beta)}$$

where $\Gamma(\beta)$ is the gamma function. The scale parameter, s, establishes the upper bound of the distribution at 1.0, and the mean of the distribution ($\theta/(\theta + \beta)$) is set to annual survival probabilities (e.g., $\exp(-M_{imm})$ of 0.91), which correspond to $M_{imm} = 0.10$. As a consequence, survival was approximated by a negatively skewed distribution. The rationale for selecting a beta distribution to model survival data is based on its simplicity, smoothness, and flexibility, making it an ideal choice for distributions that have restricted support (i.e., whose range is limited), in this case between 0 and 1 (Johnson et al. 1994).

Postreproductive mortality, M_{mat}, was assumed to differ with age at maturity. There is considerable evidence to suggest that earlier maturing individuals suffer higher survival costs of reproduction than later maturing individuals (e.g., Beverton et al. 1994; Hutchings 1994; Schultz and Conover 1999). This seems to be particularly true when early maturity is accompanied by smaller body size (e.g., Festa-Bianchet et al. 1998). Disproportionately higher survival costs experienced by smaller individuals can be attributed to energetic constraints imposed by metabolic allometry. Smaller individuals utilize proportionately more energy to maintain basal metabolic rate than larger individuals (Schmidt-Nielsen 1984). In addition, for a given expenditure of energy, larger individuals can be expected to bear lower costs because of their higher lipid reserves (e.g., Brett et al. 1969; Elliott 1976; Schultz and Conover 1999).

Among fishes, evidence that M_{mat} declines as age at maturity increases has been documented for several species, including brook trout (*Salvelinus fontinalis*) (Hutchings 1994), Atlantic silverside (*Menidia menidia*) (Schultz and Conover 1999), sand goby (*Pomatoschistus minutus*) (Lindström 1998), and threespine stickleback (*Gasterosteus aculeatus*) (Dufresne et al. 1990). There are also empirical data to suggest that M_{mat} is negatively related to age at maturity in Atlantic cod. Based on their exhaustive examination of Northeast Arctic cod otoliths collected from the 1930s, 1940s, and 1950s, Beverton et al. (1994) concluded that M declines as age at maturity increases. Specifically, they reported that M was equal to 0.25, 0.17, and 0.15 for individuals maturing at ages 6, 7, and 8 years, respectively.

I used Beverton et al.'s (1994) estimates to incorporate a higher postreproductive mortality for early-maturing individuals, given the absence of such estimates for Northwest Atlantic cod. I first converted their estimates of instantaneous rates of mortality for individuals maturing at age x to mortality probabilities (i.e., $1 - \exp(-M_{mat(\alpha=x)})$ equalled 0.22, 0.16, and 0.14 for $\alpha = 6$, 7, and 8 years, respectively). Prior to their collapse in the early 1990s, the natural mortality rate, M, of Northwest Atlantic cod was assumed to be 0.20 (Pinhorn 1975). Based on this estimate, it seemed reasonable to let $M_{mat(\alpha=6)} = 0.20$ in the simulations, which corresponds to an annual mortality rate of 18%. I then estimated postreproductive mortality for individuals maturing at age 4 in two ways. Using the ratios of mortality rates estimated by Beverton et al. (1994) (i.e., 0.22/0.14 and 0.22/0.16) and multiplying these by 0.18, I let the instantaneous rates of natural mortality for cod maturing at age 4 ($M_{mat(\alpha=4)}$) be 0.34 and 0.30, respectively. To be consistent with Beverton et al.'s (1994) results, individuals maturing at age 4 experi-

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enced these elevated rates of natural mortality each year until death.

Age-specific fecundity, m_z

Age-specific fecundity is a function of growth rate, reflected by changes to body weight with age, and to a first approximation by the number of eggs produced per unit body weight. Weights at age subsequent to maturity were calculated by multiplying the average weight at maturity, w_α, by the expected age-specific increase in body size between ages α and $\alpha + 1$ year (i.e., $w_{\alpha+1}/w_\alpha$) to obtain an estimate of weight at age $\alpha + 1$ year and then multiplying this estimate of weight at age $\alpha + 1$ year by $w_{\alpha+2}/w_{\alpha+1}$ to obtain an estimate of weight at age $\alpha + 2$ years and so on until the simulated age at death, 21 years. Estimates of $w_{\alpha+1}/w_\alpha$ were calculated from data provided by Lilly (1997) and Murphy et al. (1997). As described by Hutchings (1999), empirical estimates of annual changes in body size among fish older than 6 years are assumed to include the reductions in growth concomitant with maturation. To account for these growth costs of maturation prior to age 6, I assumed the percent reduction in annual growth rate to be equal to the proportional allocation of body tissue to gonads, as determined from estimates provided by McIntyre and Hutchings (2003). Based on these data, weights at maturity for cod maturing at ages 4 and 6 were 1.12 and 2.06 kg, respectively. The natural variability associated with individual increases in weight, ε_w, was assumed to be normally distributed with the standard deviation of each age-specific error distribution set equal to the standard deviation of the observed annual mean increases in weight at age (w_{z+1}/w_z).

Within some populations of Atlantic cod, reductions in size at maturity have been substantive. As discussed in more detail below, length at maturity among eastern Scotian Shelf cod has declined from approximately 42 cm in the late 1970s to 32 cm in the early 2000s (Fanning et al. 2003). These length reductions correspond roughly to a decline in weight from 700 to 500 g (Fanning et al. 2003). To examine how a reduction in size at maturity, independent of a decline in age at maturity, might affect population growth, I reduced weight at maturity (w_α) in the simulations by 200 g relative to those observed. Given the small lengths of the cod (32–42 cm) used to derive this empirically based reduction, such a decline in size at maturity can be considered conservative, given that the reduction in weight corresponding to a similar absolute decline in length for larger fish would be proportionately greater.

Numbers of eggs per female in Atlantic cod, as with most fishes, depend primarily on body weight (e.g., McIntyre and Hutchings 2003). Fecundity estimates were based on May's (1967) fecundity–weight relationship for cod collected from several locations off northeastern Newfoundland and modified, as described by Hutchings (1999), to yield the following association between age-specific fecundity, m_z, and age-specific weight:

$$(5) \qquad m_z = [0.48[(w_z + 0.37)/1.45] + 0.12] \times 10^6$$

Age and size at maturity

The simulations presented here are used to evaluate the consequences to population growth rate of reductions in age at maturity from 6 to 4 years and reductions in weight at maturity of 200 g. To assess the degree to which these changes reflect those observed in the wild, I present data for two cod stocks in the Northwest Atlantic: northern cod, whose geographical range extends from Labrador southeast to the northern half of Grand Bank, and eastern Scotian Shelf cod, which inhabit the waters from Halifax north to Cape Breton. Age at 50% maturity for northern cod has been estimated by Canadian Department of Fisheries and Oceans scientists (Lilly et al. 2001, 2003). The most reliable of these data are those for the years extending back to the late 1970s – early 1980s; these data were obtained from random samples collected by fisheries-independent surveys. Age at maturity estimates for previous years were calculated from various combinations of surveys (G.R. Lilly, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, NL A1C 5X1, Canada, personal communication). As a consequence, these earlier data should be treated with some caution because it is not known whether they represent truly random samples. Having said that, the similarity in age at maturity estimates immediately prior to and following the initiation of the fisheries-independent surveys throughout the range of northern cod in 1981 (Fig. 1*a*) suggests that the earlier estimates may not be unduly misleading (with the possible exception of data based on the 1973 samples). Age and length at maturity for eastern Scotian Shelf cod were estimated by Fanning et al. (2003). Estimates of prereproductive growth rate presented here for each of the stocks were calculated from length at age data compiled by Lilly et al. (2001) and Fanning et al. (2003) for northern cod and eastern Scotian Shelf cod, respectively.

Parity-dependent fertilization success

There is experimental evidence to suggest that spawning success in Atlantic cod depends on parity (i.e., the number of times an individual has produced offspring), such that individuals reproducing for the first time produce considerably fewer offspring per reproductive bout than individuals that have spawned at least once in their lives. Based on a comparison of hatching success in the laboratory, Trippel (1998) reported that hatching rates of first-time spawners were 20% of those of females that had previously spawned. To account for the possibility that spawning success is lower at maturity than at later ages, I varied egg $\text{survival}_{\text{first-time spawners}}/\text{egg survival}_{\text{others}}$ from 0.2 to 1.0.

Results

Changes to life history traits in Atlantic cod

Reductions in abundance of 99% and 92% have been associated with significant changes in life history among northern cod and eastern Scotian Shelf cod, respectively (Figs. 1 and 2). Within the former stock, age at 50% maturity among females has declined approximately 1 year since the late 1970s and early 1980s (Fig. 1*a*). Comparing maturity estimates on northern cod sampled in the early 1960s with those in recent years, age at maturity may have declined by as much as 2 years. Growth rate during prereproductive ages for northern cod is represented by the proportional increase in length between 3 and 4 years of age. From 1978 to 1999, the observed reduction in age at maturity was not accompa-

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Fig. 1. Temporal changes in (*a*) age at maturity and (*b*) prereproductive growth for northern cod (*Gadus morhua*). The former represent data on age at 50% maturity for females presented by Lilly et al. (2003); the latter represent changes in the proportional increase in length between ages 3 and 4 years, as calculated from data provided by Lilly et al. (2001). Prereproductive growth rate data are presented separately for North Atlantic Fisheries Organization (NAFO) divisions 2J (△), 3K (●), and 3L (▲).

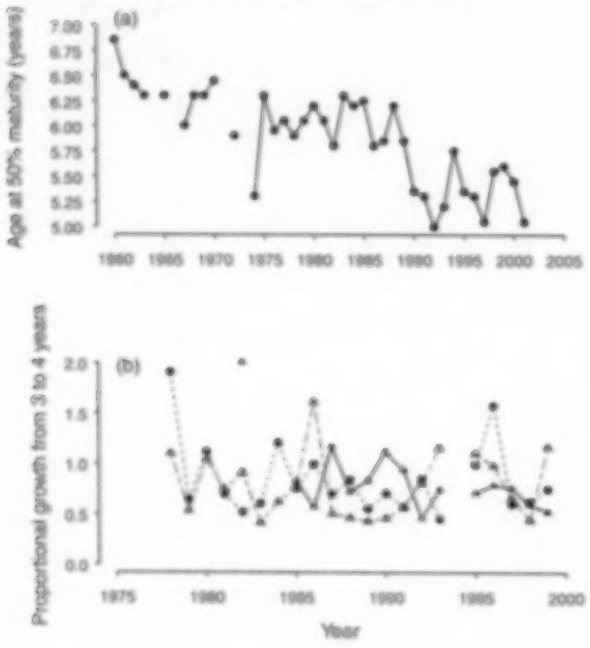
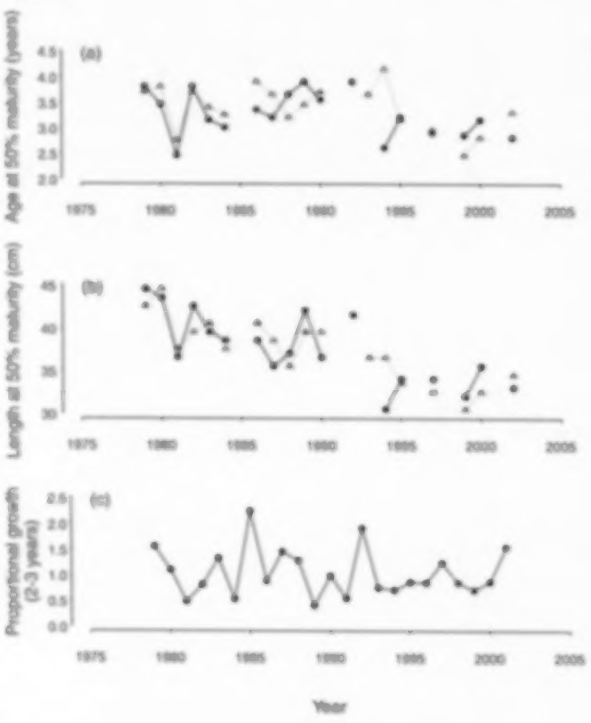


Fig. 2. Temporal changes in (*a*) age at maturity, (*b*) length at maturity, and (*c*) prereproductive growth for Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf (data are from Fanning et al. 2003). Data on age and size at maturity are presented separately for cod found in North Atlantic Fisheries Organization (NAFO) divisions 4Vs (●) and 4W (▲). Prereproductive growth represents the proportional increase in length between ages 2 and 3 years.



nied by a discernable trend in prereproductive growth (Fig. 1*b*).

Eastern Scotian Shelf cod also experienced a decline in age at maturity of approximately 1 year from the late 1970s to the late 1990s – early 2000s (Fig. 2*a*). However, given the younger reproductive ages among these cod, this 1-year reduction represents a greater proportional decline than that experienced by northern cod. Eastern Scotian Shelf cod have also experienced considerable reductions in length at maturity (Fig. 2*b*). In the eastern portion of the stock's range (Northwest Atlantic Fisheries Organization division 4Vs), length at maturity has declined from 42 to 36 cm since 1979. In the western portion of the stock's range (division 4W), the reduction from 40 to 32 cm is even greater. As with northern cod, these changes in life history were not associated with an obvious temporal trend in prereproductive growth, represented for eastern Scotian Shelf cod as the proportional increase in length between ages 2 and 3 years (Fig. 2*c*).

Influence of reduced age and size at maturity on population growth

Population growth rate declines with age at maturity. At best, when relative hatching rate is independent of parity, the reduction in r associated with earlier maturity is comparatively small (Fig. 3*a*). Among cod maturing at 6 years, r = 0.155 (16.8% per annum) as compared with the estimates of 0.146 (15.7%) and 0.136 (14.6%) for cod maturing at age 4 years and experiencing postreproductive mortality rates, M_{max}, of 0.30 and 0.34, respectively. However, as the hatching rate of first-time spawners declines relative to that of later spawners, the reduction in r associated with earlier maturity progressively increases. For example, at the relative hatching rate of 0.2 reported by Trippel (1998), r declines from 0.143 (15.4% per annum) at α = 6 years to 0.130 (13.9%) and 0.111 (11.7%) at α = 4 years.

Not surprisingly, reductions in size at maturity exacerbate the reductions in population growth affected by earlier maturity (compare the estimates of r in Figs. 3*a* and 3*b*). When size at maturity is reduced by 200 g for cod maturing at age 4 and 6 years, r declines from 0.145 (15.6% per annum) at α = 6 years to 0.131 (14.0%) and 0.127 (13.5%) at α = 4 years when hatching rate is independent of parity. However, at the relative hatching rate of 0.2, earlier maturity has an even greater impact on population growth, with r declining from 0.134 (14.3% per annum) at α = 6 years to 0.114 (12.1%) and 0.097 (10.2%) at α = 4 years.

The reduction in population growth generated by earlier age and smaller size at maturity is perhaps more dramatically reflected by changes to the probability of experiencing negative growth on a per-generation basis, which would result in declining abundance. Under the most favourable sce-

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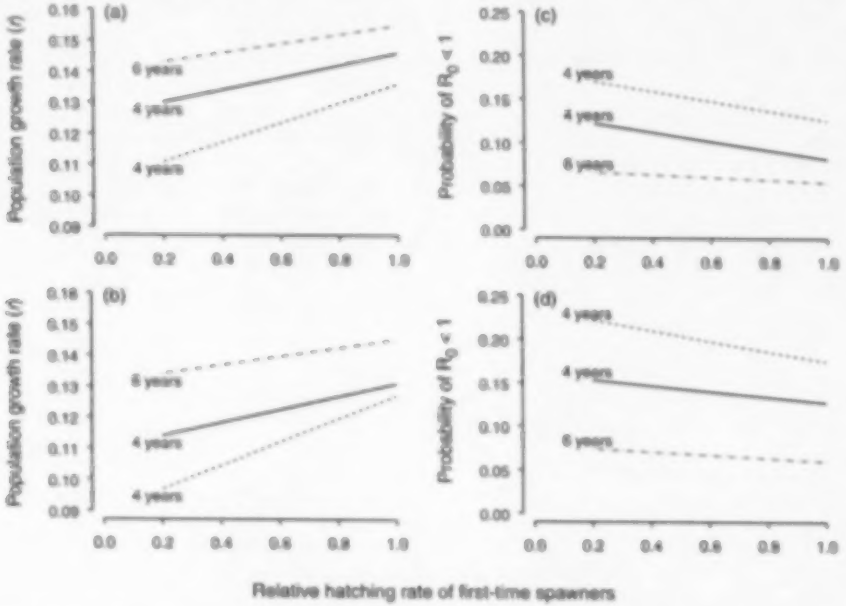
Fig. 3. Atlantic cod (*Gadus morhua*) (*a* and *b*) population growth rate, *r*, and (*c* and *d*) the probability of negative per-generation population growth ($Pr(R_0 < 1)$) as functions of age at maturity, size at maturity, and parity effects on hatching rate represented by egg $survival_{first\text{-}time\ spawners}$/egg $survival_{others}$. For cod maturing at age 4 years, the solid lines in each panel are those for which postreproductive mortality, M_{mat}, was 0.30; the broken lines are those for which $M_{mat} = 0.34$. The effects of smaller size at maturity on *r* and $Pr(R_0 < 1)$ are presented in Figs. 3*b* and 3*d*.



nario, when hatching rate was independent of parity, $Pr(R_0 < 1)$ increased from 5.5% at $\alpha = 6$ years to 8.2% and 14.5% at $\alpha = 4$ years (Fig. 3*c*). At a relative hatching rate of 0.2 (Trippel 1998), the probability of negative growth ranged from 6.6% among cod maturing at 6 years to 17.5% for cod maturing at 4 years and for which $M_{mat} = 0.34$.

Reductions in size at maturity increased the probability of negative growth even further. At the relative hatching rates for first-time spawners documented by Trippel (1998), and when $M_{mat(\alpha=4)} = 0.34$, earlier maturity more than trebles the probability of per-generation declines in abundance (compare the left-most point of the line corresponding to $\alpha = 6$ with the left-most point of the broken line corresponding to $\alpha = 4$ in Fig. 3*d*).

Discussion

Historical declines in the abundance of two Northwest Atlantic populations of Atlantic cod have been associated with changes in two life history traits of fundamental importance to population growth. These declines cannot be parsimoniously explained as phenotypic responses to reductions in population density. Rather the data are consistent with the hypothesis that earlier age and smaller size at maturity are best explained as genetic responses to fishing-induced selection against late-maturing, and large-maturing, genotypes (Hutchings 1999; Olsen et al. 2004, 2005). The primary objective of the present study was then to explore the degree to which these life history changes, irrespective of the reasons for them, might affect population growth and, thus, rate of recovery.

Overexploitation of Northwest Atlantic cod has been associated with significant reductions in age and size at maturity in most stocks (Trippel et al. 1997). Among these, northern cod have experienced a reduction in age at maturity of at least 16% (comparing the early 1980s with the early 2000s) and possibly as much as 22% since the early 1960s. Among eastern Scotian Shelf cod, age at maturity declined almost 30% between the late 1970s and the early 2000s. Concomitant with the change in age at maturity in this stock was a 20% reduction in length at maturity. Given that these stocks have sustained fishing mortality for a considerably longer period of time than that for which life history data are available, the patterns evident in the past 20–40 years may well represent declines initiated several decades earlier.

The question of whether these changes are primarily genetic or phenotypic in origin is a fundamentally important one. Phenotypically plastic responses in life history to changes in density are readily reversible, comparatively speaking. For example, if earlier maturity is a response to increased prereproductive individual growth brought about by reduced competition, then the higher densities associated with population recovery will effect a slowing of individual growth and an older age at first reproduction. By comparison, genetic responses to exploitation are relatively slow to change, particularly in the absence of strong selective pressures akin to those produced by fishing (Law 2000).

There is good reason to believe that the reductions in age and size at maturity documented for some Northwest Atlantic cod stocks can be partly explained as genetic responses to fishing-induced selection against late-maturing, and larger-maturing, genotypes (Hutchings 1999; Olsen et al. 2004). Phenotypic changes to age at maturity are almost always ac-

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companied by changes to individual growth and (or) condition, such that faster growth and increased condition lead to earlier reproduction (Policansky 1993; Roff 2002). There is no evidence that condition has improved among northern or eastern Scotian Shelf cod in the past few decades; if anything, the opposite may be true (e.g., Drinkwater 2002). As the data presented here indicate, there is no evidence that reductions in either age or size at maturity have been associated with increased growth during prereproductive ages. Thus, the most parsimonious explanation for the observed changes in traits whose heritability has been documented repeatedly in fishes (Hutchings 2002; Roff 2002) is that the changes are primarily genetic in nature.

The simulations presented here, based on a stochastic, age-structured life history model, suggest that earlier age and smaller size at maturity can have negative consequences for population growth, and rate of recovery, in Atlantic cod. These reductions in r increase with the magnitude of the survival cost of reproduction associated with earlier maturity and with reductions in the relative hatching rate of virgin spawners. At the higher of the two survival costs considered here for $\alpha = 4$ years, and at the relative hatching rates documented by Trippel (1998), a reduction in age at maturity from 6 to 4 years is associated with a 24% reduction in annual population growth; the reduction in population growth increases to 29% when size at maturity declines as well. The negative effects on recovery of lower age and size at maturity are further reflected by the increased probability of negative per-generation growth, reductions in age at maturity from 6 to 4 years more than doubling the likelihood of population decline.

The reduction in r associated with earlier age and smaller size at maturity raises the question of whether the increased natural mortality observed among some Northwest Atlantic cod stocks in recent years (Smedbol et al. 2002) can be partly attributable to changes in life history. The ubiquity of reproductive costs (Roff 2002), coupled with the likelihood that these costs increase as age and size at maturity decline, suggests that recent increases in M, often attributable to ecosystem-level changes in the strength of interspecific interactions (such as predation and competition), might be partly a function of fishing-induced changes to life history.

The present study differs from previous life history analyses of this species (e.g., Myers and Doyle 1983; Trippel et al. 1995; Hutchings 1999) in that it allows the survival cost of reproduction to increase with reductions in age at maturity. The theoretical basis for such a reciprocal relationship, based on constraints imposed by metabolic allometry, appears sound (Schmidt-Nielsen 1984). However, notwithstanding the taxonomic breadth of its empirical basis (Hutchings 2002), Beverton et al.'s (1994) study of Atlantic cod is the only one available for this species and, to my knowledge, the only study of survival costs for a commercially exploited marine fish. The paucity of such work needs to be remedied, given the intimate association between survival costs and population growth rate.

In the context of the present study, the survival costs incorporated here may well have been underestimated, having been based on estimates of M for Northeast Arctic cod, which mature at considerably larger sizes (68–80 cm; Beverton et al. 1994) than northern cod (Lilly et al. 2001) and eastern Scotian Shelf cod (Fanning et al. 2003). Similarly, the reduction in size at maturity used here (200 g) is not particularly large, based as it is on the reduction in weight observed among eastern Scotian Shelf cod, a stock with a comparatively small size at maturity. As a consequence, the reductions in r documented here for earlier maturity and smaller size at maturity may well have been underestimated. Further compounding any negative effects of smaller body size on r is the potential for reduced offspring survival owing to the production of smaller eggs (Murawski et al. 2001) and increased variability in recruitment (Hutchings and Myers 1993).

The weaknesses of any modelling approach ultimately lie in the empirical bases, or lack thereof, of the model parameters. The parameter values used here were estimated from data collected from the field. With the exception of the beta distributions used to model the error in survival, the same was true for the error distributions applied to each parameter. One limitation inherent in a previous application of this modelling approach (Hutchings 1999) has been remedied here. By allowing for a reduction in age-specific fecundity of virgin spawners relative to previous spawners, the model incorporates the finding that hatching rate among first-time spawners may be as low as one fifth that of second-time spawners (Trippel 1998). As the simulations presented here suggest, such an effect, if manifested in the field as well as the laboratory, can have a dramatic influence on population growth (also see Murawski et al. 2001). Of importance to the recovery of depleted stocks for which age and size at maturity have declined is the observation that the reduction in r associated with reduced hatching rate among virgin spawners increases as α declines and as M_{max} increases.

One additional simplification of note is the fact that the model used here did not incorporate any effects of density on age-specific survival or fecundity. Potentially the most important density-dependent effect would be on the probability of survival from birth to age 3 years, l_3. However, inclusion of such a density-dependent influence would not alter the main conclusions drawn here that reductions in age and size at maturity can negatively influence population growth, although absolute estimates of r would be adjusted upward. On the other hand, given that demographic stochasticity and environmental stochasticity on life history parameters almost certainly increase as population size declines (Lande et al. 2003), stochastically based estimates of r might, in fact, result in lower rates of population growth than those estimated here, even if weak density-dependent effects on offspring survival are included in the model.

Random variation in population growth rate can have seriously destabilizing effects on population dynamics, even though the expected population size may increase with time (Lewontin and Cohen 1969; Roff 1974). These destabilizing effects can be expected to be greater in small populations than in large ones (Lande et al. 2003). To some degree, the use of a stochastic, age-structured life history model captures these effects, perhaps most evidently when estimating the likelihood that a population will achieve particular rates of growth (e.g., $\Pr(R_0 < 1)$).

The present study draws attention to a factor rarely considered to have a major influence on recovery in severely depleted marine fishes (Hutchings and Reynolds 2004). It would

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be instructive to quantify life history changes at the population level concomitant with overexploitation for a broad range of fishes (Hutchings and Baum 2005), to assess the degree to which these changes represent phenotypic or genetic responses to fishing, and to evaluate the influence that these changes may have on population growth rate, independent of changes to fishing pressure, species interactions, and other correlates of recovery.

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Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)?[1]

A.D. Rijnsdorp, R.E. Grift, and S.B.M. Kraak

Abstract: Life history theory predicts that fishing may select for increased reproductive investment. A model of the reaction norm for reproductive investment in a capital breeder was developed to disentangle changes in reproductive investment from changes in growth rate in North Sea plaice (*Pleuronectes platessa*). Trends in reproductive investment since 1960 were estimated as (*i*) the decrease in body weight of mature males and females between the start and end of the spawning period, (*ii*) the difference in weight of ripe and spent females, and (*iii*) the ovary weight of prespawning females. These estimates were related to somatic growth estimated by back-calculation of otoliths and temperature. The ovary weight and weight loss of females that had just started and just finished spawning did not reveal any trends. There was a significant increase in weight loss over the spawning season in both sexes, but much of this increase was likely due to changes in environmental conditions. Evidence for a fisheries-induced change in reproductive investment from our analyses thus remained inconclusive. However, fecundity and ovary-weight data from previous studies tentatively suggest that an increase in reproductive investment occurred between the late 1940s and the 1960s. Such an increase is consistent with a fisheries-induced evolutionary change.

Résumé : La théorie démographique prédit que la pêche peut entraîner une sélection d'investissements reproductifs accrus. Nous avons mis au point un modèle de la norme de réaction pour l'investissement reproductif chez la plie (*Pleuronectes platessa*), un animal qui se reproduit en utilisant ses réserves énergétiques (« capital breeder »), afin de séparer les changements de l'investissement reproductif des ceux du taux de croissance. Les tendances dans l'investissement reproductif depuis 1960 ont pu être estimées en mesurant (*i*) la diminution de masse corporelle entre le début et la fin de la période de fraie chez les mâles et les femelles matures, (*ii*) la différence de masse entre les femelles pleines d'oeufs et celles qui ont frayé et (*iii*) la masse des ovaires des femelles avant la fraie. Ces estimations ont été mises en relation avec la croissance somatique estimée par rétro-calcul des otolithes et d'après la température. La masse des ovaires et la perte de masse des femelles entre le tout début et la toute fin de la fraie ne suivent aucune tendance. Il y a une augmentation significative de la perte de masse durant la saison de fraie chez les deux sexes, mais une partie importante de cette augmentation est vraisemblablement due aux changements des conditions du milieu. Nos analyses ne fournissent pas d'indice clair que la pêche génère un changement dans l'investissement reproductif. Néanmoins, des données de fécondité et de masse ovarienne provenant d'études antérieures indiquent de façon provisoire qu'il y a eu une augmentation de l'investissement reproductif entre la fin des années 1940 et les années 1960. Une telle augmentation serait compatible avec un changement évolutif causé par la pêche.

[Traduit par la Rédaction]

Introduction

Fisheries act as a selective force because of the increase in mortality rate for individuals above the size at first capture. Life history theory predicts that the changed mortality schedules may select for earlier maturation, increased reproductive investment, and a change in growth rate (Roff 1992; Stokes et al. 1993; Law 2000). Support for some of these predictions is available from experiments (Reznick et al. 1990; Conover and Munch 2002), but for wild populations it is often difficult to disentangle the genetic response from the phenotypic response to concurrent changes in environmental conditions (Rijnsdorp 1993*a*; Heino et al. 2002).

Changes in maturation have been reported in several species (Rijnsdorp 1989; Jørgenson 1990; Trippel 1995). Applying the reaction-norm approach for maturation (Stearns

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A.D. Rijnsdorp,[2] R.E. Grift, and S.B.M. Kraak. Netherlands Institute for Fisheries Research, Animal Sciences Group, Wageningen University and Research Centre, P.O. Box 68, 1970 AB IJmuiden, the Netherlands.

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[2]Corresponding author (e-mail: adriaan.rijnsdorp@wur.nl).

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Table 1. Mean lengths, mean ages, and numbers of North Sea plaice (*Pleuronectes platessa*) sampled for weight, and the numbers of market samples taken between December and March during the period 1960–2002.

	Length (cm)		Age (years)			
	Mean	SD	Mean	SD	No. of fish	No. of samples
Adult males	33.0	4.0	4.9	1.9	56 193	1915
Adult females	41.2	6.2	7.4	3.3	65 482	1964
Juvenile females	30.5	2.7	3.4	1.0	12 971	1777

and Koella 1986), it has been convincingly shown that observed changes in the onset of maturation can be at least partly due to genetic selection (Heino et al. 2002; Grift et al. 2003; Barot et al. 2004). With regard to long-term changes in growth, changes in size have been reported in Pacific salmon (*Oncorhynchus* spp.; Ricker 1981), of which the decrease in length of pink salmon (*Oncorhynchus gorbuscha*) at age 2 could be ascribed to a fisheries-induced decrease in growth rate (Ricker et al. 1978). In a careful analysis of back-calculated individual growth rates of cod (*Gadus morhua*), Sinclair et al. (2002) were able to show different selection regimes favoring fast growth in the 1970s and slow growth in the late 1980s and 1990s. The continued small size at age around 2000 was consistent with a genetic response to the size-selective mortality imposed by the fishery in the 1990s.

We do not know of any field study that addresses the hypothesis of a fisheries-induced change in resource allocation to reproductive effort. Differences in reproductive investment were reported among cod populations that were considered to be adaptive to local environments (McIntyre and Hutchings 2003). Fish may show plasticity in energy allocation between growth and reproduction in response to the predictability of food resources (Siems and Spikes 1998). Increased allocation of energy to reproduction can be reflected in an increase in the gonadosomatic index (or fecundity), but may also be reflected in the decline in postspawning condition if fish increase their reproductive investment through increased depletion of their energy reserves. In both cases the increase in reproductive investment will result in a decrease in somatic growth (Heino and Kaitala 1999).

North Sea plaice (*Pleuronectes platessa*) exhibit historical trends toward earlier maturation that are consistent with a fisheries-induced adaptive change (Rijnsdorp 1993*a*, 1993*b*; Grift et al. 2003). In this paper we extend our analysis of fisheries-induced change in North Sea plaice and focus on trends in reproductive investment. Reproductive investment is estimated as (*i*) the weight loss of adult fish during the spawning period, (*ii*) the difference in weight between ripe and spent females, and (*iii*) prespawning ovary weight. A reaction norm for reproductive investment is developed to disentangle a time trend in reproductive investment from phenotypic plasticity.

Material and methods

Biology of plaice

The plaice is an iteroparous broadcast spawner with clear sexual dimorphism in growth and reproductive characteristics (Rijnsdorp and Ibelings 1989) that has been exploited intensively for more than a century (Rijnsdorp and Millner 1996). Spawning in the North Sea occurs between December and early April over a large offshore area extending from the English Channel into the southern and central North Sea and the Skagerak and Kattegat (Houghton and Harding 1975; Harding et al. 1978; Nielsen et al. 2004). The time of peak spawning shifts with increasing latitude. The plaice is a capital spawner that does not feed during the spawning period (Todd 1914; Rijnsdorp 1989; Fonds et al. 1992) and reproductive investment is supported from the energy reserves laid down in the body (Dawson and Grimm 1980; Rijnsdorp and Ibelings 1989; Rijnsdorp 1990).

Sampling

Regular samples of plaice from commercial North Sea landings have been collected since 1960. The landings of the Dutch fleet cover the major spawning areas in the southern and central North Sea and can be considered representative of the entire population (Rijnsdorp 1989). Until the late 1970s, a market sample comprised 70 individual plaice taken at random from the unsorted catch, and 20 fish of each of the four market categories (27–34, 34–38, 38–41, and >41 cm length) since then. In the laboratory, length, weight, sex, and maturity stage (only in spawning months) were determined and the otoliths were collected for age determination. For the spawning seasons 1982–2002 (December–March), ovary weights were recorded. Data for years in which only part of the spawning period was covered (1964, 1967, 1985, 1988, 1992, 1995) were not included in the analysis. A total of 7091 ovary weights of females with ripening ovaries (maturity stage 2) were analyzed. The number of plaice sampled for weight and their mean length and age are provided in Table 1. The number of annual market samples varied between 25 and 120, except in 1962 and 1964–1966, when only 6–9 market samples were taken. No data on juvenile males were available because they mature before they appear in the landings. To illustrate the distribution of the samples over the spawning season and the trends in weight during this period, the mean condition factor ($K = WL^{-3}$, where W is weight and L is length), of adult females per market sample versus the sampling date (day number) for 3 years is shown in Fig. 1. Sampling intensity was generally lower in December than from January to March. The mean length and age of sampled fish gradually decreased after 1960 because they did so in the landings. Adult female length decreased from 40.6–44.1 cm (7.9–9.7 years) in the 1960s to 39.5–40.6 cm (5.6–7.2 years) in the 1990s. Adult male length decreased from 32.1–34.7 cm (4.9–6.0 years) in the 1960s to

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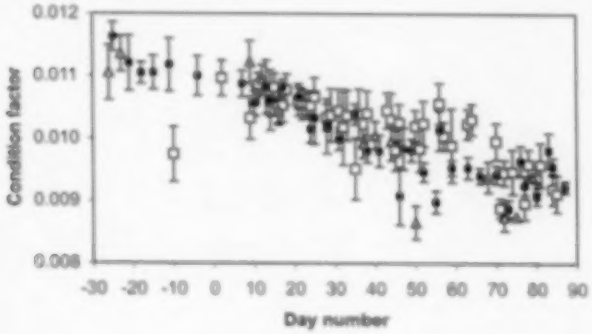
Fig. 1. Mean and 95% confidence limits of the condition factor ($g \cdot cm^{-3}$) for adult female North Sea plaice (*Pleuronectes platessa*) per market sample between December and March in 3 individual years, 1963 (□), 1977 (■), and 1998 (△). Day number is relative to 1 January.



31.3–32.1 cm (4.1–5.2 years) in the 1990s. No clear trend in mean length and age of juvenile females was apparent.

Plaice maturity stages are described in Rijnsdorp (1989) and consist of an immature stage (maturity stage 1), a ripening stage (maturity stage 2), a spawning stage (2 < maturity < 6), and a spent stage (maturity stage ≥6). Within the spawning stage, fish at maturity stage 3 can be distinguished as having a full ovary with a few hyaline eggs representing the start of spawning. The timing of spawning is reflected in the gradual transition of adult fish between successive maturity stages (Fig. 2). The spawning season started in December (day –30) and ran to 1 April (day 90). We applied 1 December as the birthdate. As most of the plaice in the market samples were gutted (only viscera removed, gonads left intact), the weight of whole fish was converted to gutted weight by applying the conversion factor 1.07.

Reproductive investment

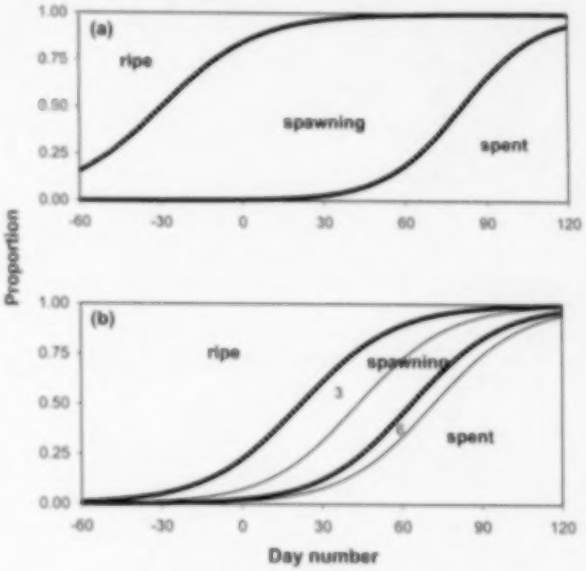
Three proxies for reproductive investment were analyzed. First, weight loss during the spawning period was estimated from the difference between mean body weight at day 0 and day 60 for adult males and adult females of standard length for the period 1960–2002. The reference dates were chosen to approximate the spawning period (Fig. 2). Second, a more detailed analysis of the change in body weight was carried out for adult females that had just started spawning (ripe, i.e., maturity stage 3) and that had just finished spawning (spent, i.e., maturity stage 6). Third, ovary weight at the peak of the spawning period (day 20) was estimated for each year for ripening females of standard length. The latter time series covered a reduced time period, 1982–2002.

In addition, data on both fecundity and somatic growth of 248 individual females from Rijnsdorp (1990) were reanalyzed to determine the relationship between fecundity and growth rate. Fecundity and somatic growth rate in the final year were standardized to that of a 40-cm female by regression of log(fecundity) on log(length) and log(length increment) on length.

Somatic growth rate

The somatic growth rate was estimated from back-calculations of lengths from annuli in otoliths of females

Fig. 2. Seasonal progression of spawning between November and April as reflected in the proportion of adult male (*a*) and female (*b*) plaice that have reached a particular maturity stage. The heavy lines indicate the proportions of fish that have reached the spawning stage (maturity stage ≥3) and the spent stage (maturity stage ≥6). The difference between the heavy and thin lines show the proportion of females that have just started spawning (maturity stage 3) and just finished spawning (maturity stage 6). The spawning ogives were estimated by logistic regression analysis for a 35-cm male and a 40-cm female at a latitude of 53°30′N using data of 1981–1985.



sampled during spawning months in the southern North Sea. The data set comprised 2939 otoliths of female plaice collected since 1960 and was an update of the sets described in Rijnsdorp and Van Leeuwen (1992, 1996) complemented with between 78 and 121 otoliths from each year between 1995 and 2002. As the annual length increment decreases with fish size, model 1 was used to estimate a growth index for each individual year (*Y*):

$$(1) \qquad \log(dL) = Y_i + L$$

where dL is the length increment in year Y (the year preceding capture) and L is the length at the start of that year. A log-transformation was employed to normalize the residuals. Because the otolith samples were stratified by length, the ratio of the number of otoliths sampled at size i and the number of plaice in the commercial landings at size i was used as a weighting factor that was assigned to the vector of back-calculated length for each individual fish. The growth index thus estimated is a proxy for the growth rate of an average fish of standard size in the population and will track the interannual variations in growth rate. This index, however, does not necessarily track changes in growth rate among age groups, as it does not take account of changes in (size-selective) mortality (Rijnsdorp 1999; Sinclair et al. 2002).

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Temperature

Monthly average sea-surface temperatures, measured at a coastal station (Den Helder), were used to estimate a temperature index representative of the temperature conditions during the growing period between April and November and during the spawning period between December and March (Fig. 3*a*). There is an overall positive trend in temperature during the spawning season (slope = 0.038 degrees·year^{-1}; $r = 0.33$, $P < 0.05$) as well as during the growing season (slope = 0.022 degrees·year^{-1}; $r = 0.45$, $P < 0.01$). Superimposed on this trend, relatively cool and warm years occur. The interannual variation in temperature during the spawning period is larger (coefficient of variation = 36%) than during the growing period (coefficient of variation = 5%). There is a positive correlation between winter and summer temperatures ($r = 0.43$, $P < 0.01$; Table 2).

Statistical analysis

Statistical analyses were carried out using the Genmod procedure in SAS (SAS Institute Inc. 1999). Ovary and body weights (W) are functions of body size (L) and will change during the spawning period (Barr 1963; Dawson and Grimm 1980; Rijnsdorp 1991). The seasonal pattern, which may be further affected by latitude (l) (Simpson 1951, 1959; Horwood et al. 1986), is described with the following general regression model:

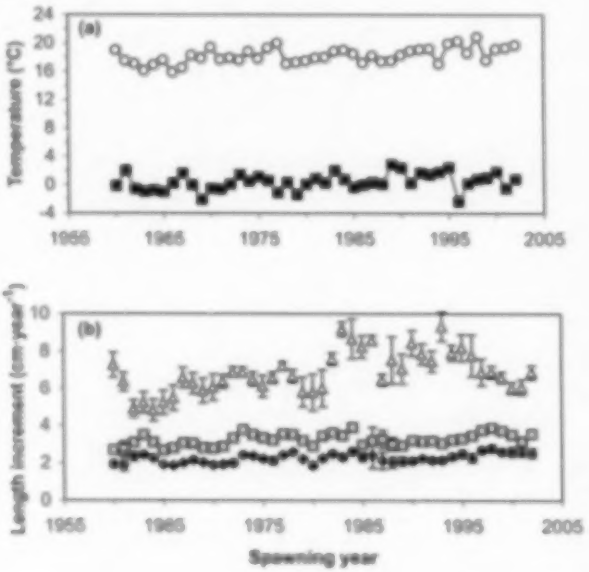
$$\log(W) = \log(L) + Y_i + Y_i \times t' + \log(L) \times t' + l + l \times t' + Y_i \times \log(L) \quad (2)$$

where t' represents a geometric series of day number with a first-, second-, and third-order term to model the seasonal pattern in each year (Y). The interaction terms with day number were included to model differences in the seasonal pattern with fish size and latitude. The log-transformation was chosen to normalize the residuals and because the effects of the variables are likely to be multiplicative rather than additive. The significance of the explanatory variables of the model was tested against the full model.

Four versions of model 2 were derived from the market-sample data: a model for the body weight of mature females, a model for the body weight of mature males, a model for the body weight of juvenile females, and a model for the ovary weights of mature females. These models (including only significant terms) were then used to estimate for each year the seasonal pattern in body (or ovary) weight for fish of a standard length at an average latitude of 53°30′N. Standard fish lengths were 35 cm for adult males, 40 cm for adult females, and 30 cm for juvenile females.

In the analysis of the body weights of females that had just started (maturity stage 3) and finished spawning (maturity stage 6), we did not model the seasonal pattern of weights. The rationale was that choosing maturity stages that coincide with the start and end of the spawning period (Fig. 2) ensured that interannual differences in the timing and duration of spawning (van der Land 1991; Rijnsdorp and Witthames 2005) would not affect the estimates of reproductive investment.

Fig. 3. (*a*) Interannual variation in sea-surface temperature at a coastal station at 53°N, 5°E during the spawning period (December–March; ■) and growing period (April–November; ○). (*b*) Annual length increments for a 20-cm (△), 35-cm (□), and 40-cm (◆) plaice, estimated using back-calculation from otolith length.



Results

Somatic growth rate

The estimated length increments of a female of 40 cm (range = 30–50 cm), 35 cm (range = 25–45 cm), and 20 cm (range = 15–25 cm) from model 1 are shown in Fig. 3*b*. These growth-rate estimates reflect interannual differences in somatic growth rate for the range of standardized lengths (30–40 cm) that we have used for our indices of reproductive investment. The growth rate of a 20-cm female reflects the growth rate of a juvenile female reaching the standard length of 30 cm in January, at the end of the growing period. The mean and standard deviation of the growth indices, as well as the correlation matrix, are provided (Table 2). The growth index shows a weak but significant positive trend of 0.0125 cm·year^{-2} ($r = 0.48$, $P < 0.01$) and 0.011 cm·year^{-2} ($r = 0.58$, $P < 0.01$) in 35- and 40-cm plaice, respectively. The growth rate of the 20-cm plaice did not show a positive trend in time ($r = 0.09$, ns).

Reproductive investment

Weight loss during spawning

The model explained between 92.5% and 95% of the variance in body weight of adult as well as juvenile plaice, with body length being the most important variable (Table 3). As a substantial part of the explained variance could not be ascribed to a single covariate (collinearity between 37% and 71%), the contribution of the individual terms was relatively small. The slope of the body weight – body length relation varied among years as reflected by the significant interaction

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Table 2. Mean and standard deviation and correlation matrix of growth indices of plaice and temperature during the study period, 1960–2002.

	Growth (cm·year^{-1})			Temperature (°C)	
	Females	Males	Juveniles	Spawning period (Dec.–Mar.)	Growing period (Apr.–Nov.)
Mean	2.27	3.25	7.24	4.01	13.39
SD	0.25	0.33	0.88	1.46	0.62
Correlation matrix					
Growth					
Females	1				
Males	0.845***	1			
Juveniles	0.137	0.326*	1		
Temperature					
Spawning season	0.043	0.027	–0.083	1	
Growing season	0.227	0.118	0.108	0.435**	1

Note: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Table 3. Percentages of the variance in body weight that can be ascribed to log(length), day number, and latitude.

	Body weight					
	Adult males	Adult females	Juvenile females	Ripe females	Spent females	Ovary weight (ripe females)
No. of observations	53 183	60 321	11 645	9600	4944	7091
Log(length)	23.247***	55.088***	33.132***	89.727***	90.791***	65.423***
Spawning year	0.144***	0.081***	0.104***	0.119***	0.204***	0.322***
Log(length) × spawning year	0.131***	0.083***	0.090***			
Day × spawning year	0.233***	0.221***	0.165***			2.889***
Day^2 × spawning year	0.056***	0.068***	0.070***			0.631***
Day^3 × spawning year	0.051***	0.059***	0.084***			
Latitude	0.083***	0.001***	0.014***	0.015***	0.009***	1.195***
Day × latitude	0.004***	0.022***	0.001			0.045**
Day^2 × latitude	0.007***	0.030***	0.003*			
Collinearity	70.975	37.450	58.879	4.600	4.547	0.273
Total	94.930	93.103	92.541	94.461	95.552	70.799

Note: The collinearity term indicates the explained variance that cannot be ascribed to a single covariate. Results are from model 2 (see the text). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

term. Latitude showed a significant interaction with day number, reflecting the differences in seasonal pattern with latitude.

The seasonal patterns in body weight were estimated for a standard fish at an average latitude (Fig. 4). The seasonal decrease in body weight is nonlinear, with the highest rate of decrease occurring in January–February. In some years, body weight still increased in December, which indicates that fish were still feeding and not yet spawning. At the end of the spawning season in March, the decrease in body weight slows down, or body weight may even start to increase. In juveniles, the amplitude of the seasonal pattern in body weight was smaller than in adults and also appears to have been more variable between years.

Weight loss between day 0 and day 60 showed considerable interannual variation, with an overall statistically significant positive trend in both adult males and females but not in juvenile females (Table 4, Fig. 5). The trends toward increasing weight loss for both adult males and females were due to statistically significant trends toward higher body weight on day 0 for both sexes, as well as weaker trends toward lower body weight on day 60 for both sexes (Table 4). For juveniles, there were no significant trends in body weight on either day 0 or day 60 (Table 4, Fig. 5). Juvenile weight, however, increased between 1960 and the early 1970s, and then decreased until the mid-1980s, after which it remained at a level just above that of the early 1960s (results not shown).

Weight loss between spawning and spent females

The body weight of females that had just started spawning (maturity stage 3) or had just finished spawning (maturity stage 6) was mainly affected by length, which accounts for 90% of the variance (Table 3). Latitude and spawning year made a small but significant contribution. Weight loss between the ripe stage and the spent stage showed interannual variation but no statistically significant trend in time (Table 4, Fig. 5*b*). Also the weight of ripe or spent females did not show a statistically significant temporal trend (Table 4).

Ovary weight

Length explained the major part of the variance in ovary weight. The variables day and latitude explained a small (<2%) but significant part of the variance, reflecting the dif-

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Fig. 4. Change in mean body weight between December 1 (day −30) and April 1 (day 90) in individual years for a standard-length adult female (*a*), adult male (*b*), and juvenile female (*c*), and seasonal change in ovary weight for an adult female (*d*). Weights are given for a standard-length plaice (adult male 35 cm; adult female 40 cm; juvenile female 30 cm) at a latitude of 53°30′N.

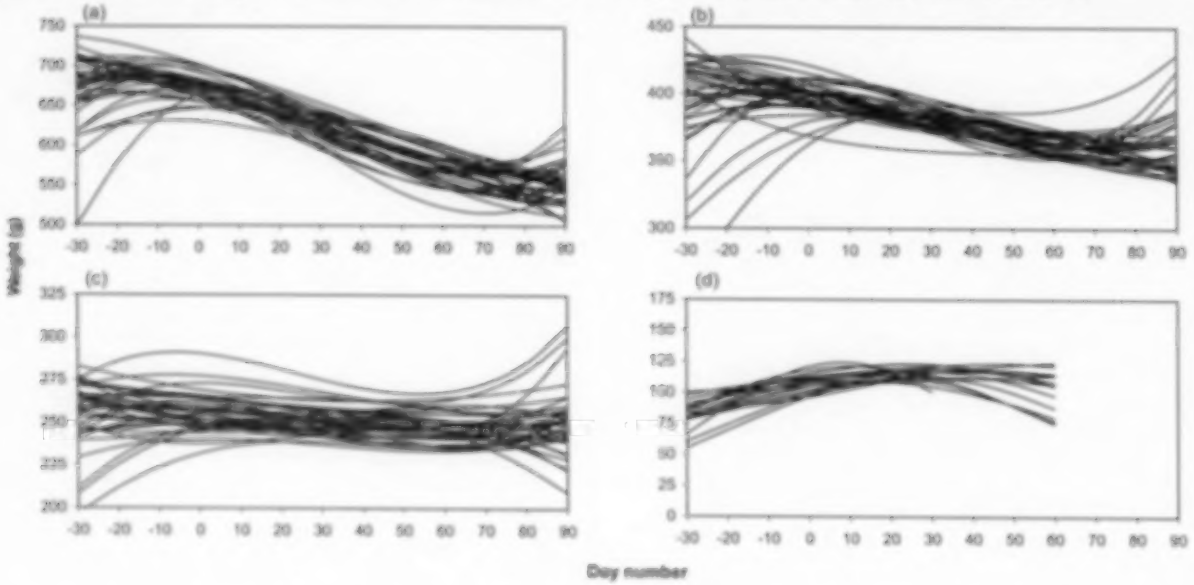

Table 4. Pairwise correlation coefficients of reproductive investment indices and year, somatic growth index, and temperature during the growing season and temperature during the spawning season.

			Temperature	
	Year	Somatic growth index	Growing season	Spawning season
Body weight				
Adult males (35 cm; n = 37)				
Day 0	0.437**	0.264	0.125	0.071
Day 60	−0.191	0.034	−0.020	−0.103
Weight loss	0.539**	0.236	0.137	0.140
Adult females (40 cm; n = 37)				
Day 0	0.527**	0.285*	0.178	0.147
Day 60	−0.390*	−0.076	−0.604**	−0.515**
Weight loss	0.666**	0.244	0.626**	0.540**
Juvenile females (30 cm; n = 37)				
Day 0	0.131	0.555**	0.268	0.156
Day 60	0.189	0.295*	0.280*	0.072
Weight loss	0.025	0.439**	0.072	0.297*
Ripe and spent females (40 cm; n = 34)				
Ripe females	0.134	0.260	0.099	0.004
Spent females	−0.015	0.166	−0.044	−0.220
Weight loss	0.137	0.056	0.137	0.240
Ovary weight (adult females, 40 cm; n = 17)	0.330	0.114	0.071	0.137

Note: *, $P < 0.05$; **, $P < 0.01$.

ferent seasonal trends in ovary weight with latitude (Table 3). Seasonal trends in ovary weight varied significantly among years. Ovary weight increased through December and reached a peak or plateau in early January (Fig. 4*d*).

The year effect reflected significant interannual variation in ovary weight. However, no statistically significant trend in ovary weight could be detected (Table 4, Fig. 5*c*).

Effects of growth and temperature on reproductive investment

A capital spawning fish may increase its reproductive investment by either increasing its body weight at the start of spawning, decreasing its weight at the end of spawning, or both. Pairwise correlation analysis (Table 4) showed that both adult males and females exhibited a positive association

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Fig. 5. Annual estimates of reproductive investment by a standard-length plaice. (*a*) Loss of body weight between day 0 and day 60 for adult males (○) and females (●) and juvenile females (×). (*b*) Weight loss by an adult female between the start (maturity stage 3) and end of spawning (maturity stage 6). (*c*) Ovary weight on day 20 for a standard-length plaice (adult male 35 cm; adult female 40 cm; juvenile female 30 cm) at a latitude of 53°30′N.

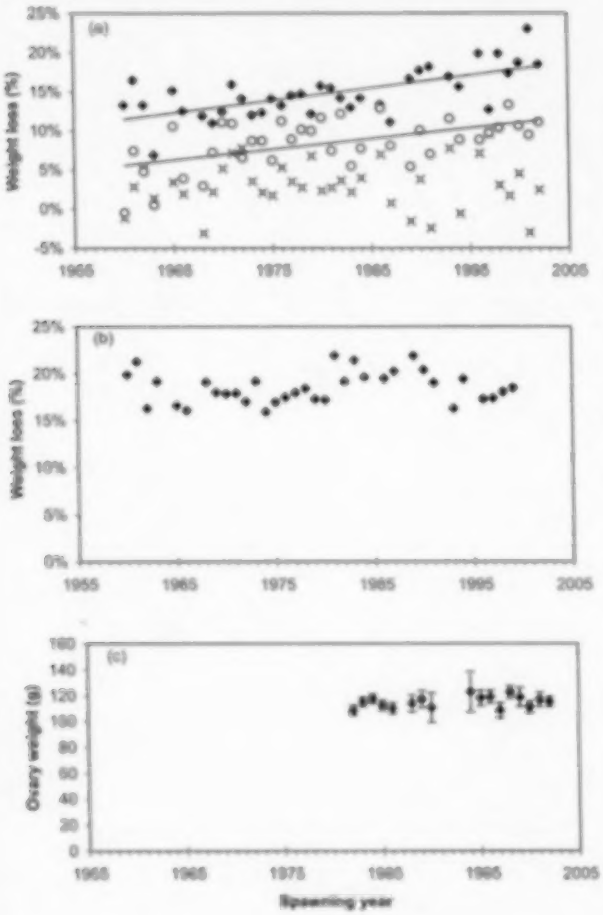
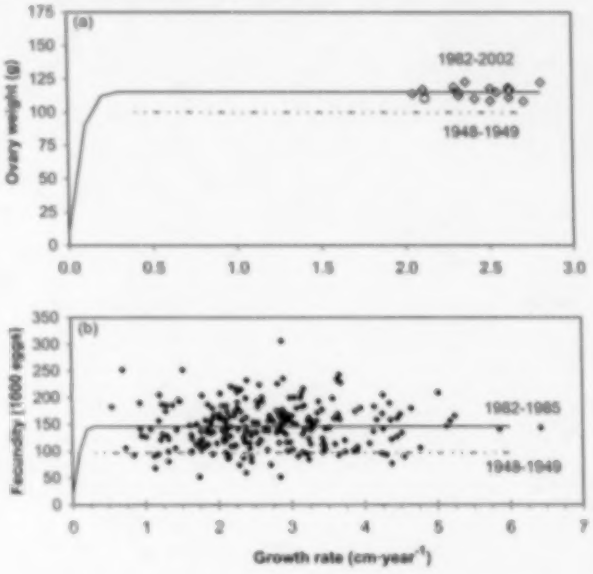


Fig. 6. Relationship between the population mean ovary weight and somatic growth rate (*a*) and fecundity and somatic growth rate (*b*) of individual female plaice. All data are standardized to a female plaice of 40 cm length. The solid lines show the reaction norms for reproductive investment; the broken lines indicate tentative reaction norms for the late 1940s. Data in *b* are reanalyzed from Rijnsdorp (1990).



between weight at the start of the spawning period and somatic growth rate. This association was statistically significant for females but not for males. Growing- and spawning-season temperatures had no effect on weight of adult fish at the start of the spawning season. In contrast, both growing- and spawning-season temperatures were negatively correlated with weights of both adult male and female at the end of the spawning season. Again these associations were statistically significant for females but not for males (Table 4). The weight of ripe and spent females showed similar correlations with growth rate and temperature, although most were weak and none were significant (Table 4).

Body weights of juveniles at both the start and end of the spawning period showed significant positive correlations with somatic growth and positive associations with both temperature indices, although only the association with end weight and growing-season temperature was statistically significant (Table 4).

Ovary weights did not show significant pairwise correlations with either growth rate or temperature (Table 4, Fig. 6*a*). Also, no relationship could be detected between the fecundity and somatic growth rate of individual females (Fig. 6*b*).

In the pairwise correlation analysis, only body weights at the start and end of the spawning season exhibited statistically significant associations with time, growth rate, and (or) temperature. Therefore, multiple regression techniques were used to examine the combined effects of growth rate, temperature, and time on these variables (Table 5): (*i*) temperature during the growing season had a significant negative effect on body weight at the start of the spawning season in both adults and juveniles; (*ii*) temperature during the spawning season had a significant negative effect on body weight at the end of the spawning season for adults but not for juveniles; (*iii*) somatic growth rate had a significant positive effect on juvenile size at both the start and end of the spawning season; it had no effect on adult size; (*iv*) no temporal trend in body weight could be detected for adults or juveniles at the start or end of the spawning season.

Discussion

Reproductive investment

In our analysis we assumed that fish were sampled randomly and independently from the population. In the case of samples from commercial fisheries this may not be true, as commercial vessels show a heterogeneous spatial distribu-

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Table 5. Results of analysis of covariance of body weights at the start and end of the spawning period in relation to somatic growth index, temperature, and year (ns, not significant).

	Adult males and females				Juvenile females			
	Percentage explained	Estimate	SE	*P*	Percentage explained	Estimate	SE	*P*
Start of spawning								
Growth rate	2.6	0.0182	0.0154	ns	26.5	0.0214	0.0057	<0.001
Temperature during growing season	7.4	–0.0188	0.0062	<0.01	8.4	–0.0151	0.0087	<0.05
Year	0.6	0.0003	0.0004	ns	0.2	–0.0001	0.0004	ns
Percentage explained	10.6				35.1			
End of spawning								
Growth rate	0.001	0.0152	0.0142	ns	13.7	0.0145	0.0059	<0.05
Temperature during spawning season	41.3	–0.0180	0.0023	<0.001	3.8	–0.0028	0.0037	ns
Year	1.4	–0.0005	0.0003	ns	6.4	–0.0007	0.0004	ns
Percentage explained	42.8				23.9			

tion that is affected not only by the distribution of the fish resource but also by socioeconomic factors (Rijnsdorp et al. 1998). Hence, the variation within market samples might be smaller than in the population, and the significance levels of tests for temporal trends and other associations may be deflated. However, since our results were highly significant, this sampling bias should not affect our conclusions.

An increase in reproductive investment may enhance the energy allocated to the production of gametes, the energy allocated to behavior, or both. In females, reproductive energy will be channelled mainly into egg production. Behavioral cost will be relatively low. An increase in reproductive investment, therefore, may be reflected in an increase in ovary weight, a decrease in postspawning body weight, or both. For males, gamete production is less costly and male reproductive investment may be expected to comprise gamete production as well as behavioral costs. Male plaice are known to show more active behavior during spawning (Solmundsson et al. 2003). As only large males have been shown to be in spawning condition throughout the spawning season (Rijnsdorp 1989), an increase in reproductive investment in smaller males may allow them to participate in spawning over a longer time period.

Weight loss is necessarily a crude proxy for reproductive investment, as it only partly reflects energy loss during spawning (Dawson and Grimm 1980). The 10% and 16% weight loss from day 0 to day 60 of the spawning season estimated in this study for males and females compares with a decrease in energy content of 27% and 44%, respectively (Rijnsdorp and Ibelings 1989). The observed interannual differences in the seasonal patterns, as well as the differences between adult males and females and juvenile females, are likely to be due to interannual differences in feeding incidence and temperature. In adult females, interannual differences in feeding incidence during the spawning season are unlikely to affect body weight at the start of spawning, as the feeding incidence of ripening females is less than 3% (Rijnsdorp 1989). However, body weight at the end of the spawning season may be affected, as spent females have already resumed feeding in January, with feeding incidence increasing from 30% in January to 100% in April. Also, in males, feeding during the spawning season may have some effect on the seasonal pattern in body weight, as they show a feeding incidence between 10% and 20%. Also, juveniles show significant feeding activity during winter, with feeding incidence increasing from a seasonal low of 30% in December to 40% in January and 65%–80% in March and April. In addition, interannual differences in water temperature will have contributed to the observed differences in the seasonal patterns in body weight. Hence, the index of reproductive investment determined from the weight loss between fixed start and end dates during the spawning season appears to be very sensitive to environmental influences.

The other two indices of reproductive investment used in this study — ovary weight and the difference in body weight between ripe and spent females — should be more reliable, since they will be less sensitive to interannual differences in feeding incidence during the spawning season, and to differences in the timing of spawning. Neither of these indices provided evidence for an increase in reproductive investment in the study period from 1960 to the present, although both metrics showed weak positive, but nonsignificant, trends in time.

Reaction norm for reproductive investment

To disentangle a genetic change in reproduction from phenotypic plasticity we need to know the factors affecting phenotypic plasticity in reproduction. In a capital spawner such as plaice, reproductive investment is dependent on the energy reserves laid down during the previous growing period (Stearns 1992; Rijnsdorp 1990), and may be affected by feeding conditions during the previous growing season (Horwood et al. 1989; Kjesbu et al. 1998; Marshall et al. 1999). Fecundity and somatic growth rate are fine-tuned to the rate of energy acquisition during the feeding season (Tyler et al. 1994; Witthames and Greer Walker 1995; Kurita et al. 2003). Under favorable feeding conditions, a fish will recover from the energy loss incurred during the previous spawning event, undergo fast somatic growth, have high oocyte recruitment, and build up energy reserves in propor-

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Table 6. Comparison of estimated mean ovary weights and fecundity during different periods for females of three lengths: 30 cm (4 years), 40 cm (6 years), and 50 cm (8 years).

	Body length (cm)			
	30	40	50	Source
Ovary weight (g)				
Southern Bight				
1948–1949	34.7	100.3	228.7	Rijnsdorp 1991
1977–1985	39.1	113.5	258.6	Rijnsdorp 1991
1982–2002	38.2	111.4	256.2	This study
Fecundity (1000 eggs)				
German Bight				
1900–1910	33.6	104.8	252.8	Rijnsdorp 1991
1977–1985	63.8	141.4	261.9	Rijnsdorp 1991
Southern Bight				
1948–1949	35.9	89.3	181.3	Rijnsdorp 1991
1977–1985	72.8	159.8	294.0	Rijnsdorp 1991

tion to its increasing body size. Under poor feeding conditions, a fish may still recover from the previous spawning event and build up the energy stores necessary for reproduction at the expense of a reduction of somatic growth, but maintain its size-specific fecundity. Only under very poor feeding conditions, if, for instance, annual energy acquisition is less than the energy loss during the previous spawning event, will size-specific fecundity decrease (Rijnsdorp 1990). With this mechanism, the reaction norm for reproductive investment can be described by a horizontal line over a wide range of somatic growth rates. Only at very low somatic growth rates will size-specific reproductive investment decrease. Variation of individual fish around this reaction norm will be due to variations in energy acquisition during the different phases of the seasonal cycle; for example, poor feeding conditions at the end of the growing period may lead to more resorption of oocytes and a reduction of size-specific fecundity.

Fisheries-induced change in reproductive investment

The evidence presented in this paper does not provide unequivocal support for the hypothesis of a positive trend in size-specific reproductive investment during the study period, 1960–2002. Although the increase in weight loss during the spawning period is in agreement with the expected fisheries-induced change in reproductive investment, the alternative explanation of a phenotypic response to an environmental change cannot be excluded and is even more likely.

Rijnsdorp (1991) reanalyzed historic data on ovary weight and fecundity of plaice and showed that the mean ovary weight was 13% higher in the early 1980s than in the late 1940s, and that fecundity has also shown an increase since the late 1940s (Table 6). The change in fecundity was particularly pronounced in 30- and 40-cm females. In 50-cm females, little increase in fecundity was observed. This is in line with expectation because females of this size already spend their whole annual energetic gain on reproduction (Rijnsdorp and Ibelings 1989; Rijnsdorp 1990). The ovary weights and fecundity observed by Simpson (1951) in the late 1940s (shown by the broken lines in Fig. 6) suggest a shift of the reaction norm to a higher level during the recent period. The somatic growth rate of a 40-cm female in the late 1940s was about 1.5 cm per year (Rijnsdorp and Van Leeuwen 1992), well below that observed in recent decades, but not yet at the level where individual data suggest that size-specific fecundity is reduced (Fig. 6*b*). The sea-surface temperature during the spawning seasons in these years was about 4.5 °C, well within the temperature range observed since 1982.

The available data on the potential fecundity of North Sea plaice (Rijnsdorp 1991) thus support the hypothesis of a fisheries-induced increase in reproductive investment in females smaller than 50 cm, although the relative increase in fecundity was much larger than the increase in ovary weight.

If the reproductive investment in plaice increased as a result of a fisheries-induced adaptive change, we would expect a reduction in somatic growth as a larger proportion of the available energy resources are channelled into reproduction (Roff 1983; Heino and Kaitala 1999). Alternatively, reproductive investment can be traded off against a higher mortality risk, e.g., in terms of decreased energy allocation to the immune system (Sheldon and Verhulst 1996; Lochmiller and Deerenberg 2000), or energy can be saved by economizing on risk-avoidance behavior (Candolin 1998). The growth rate of >35-cm plaice did not show a trend before the 1970s (Rijnsdorp and Van Leeuwen 1992). Also no change in the somatic growth rate of larger size classes of plaice was observed in a comparison of otolith growth patterns in medieval and recent samples (Bolle et al. 2004). A fisheries-induced decrease in somatic growth of adult plaice, however, may be confounded by an increase in growth due to a release in density-dependent growth. The positive trend observed in this study is likely due to the increase in the fishing mortality rate since the 1960s (Rijnsdorp 1999).

The lack of clear evidence for a positive trend in reproductive investment since 1960 contrasts with the strong evidence for a fisheries-induced shift in the reaction norm for maturation observed in the same data set (Grift et al. 2003). This contrast poses the question whether phenotypic variability is confounding an underlying genetic change in reproductive investment. Although we have attempted to correct for phenotypic variability, the approach taken was necessarily crude. No data are available on the effect of interseasonal differences in feeding conditions, which may confound a change in the reaction norm. Also, no insight into the effect of temperature or population density on reproductive investment is available.

On the other hand, further increases in reproductive investment may be constrained by the increase in mortality cost of reproduction (Roff 1992). In flatfish, postspawning condition decreases with fish size and may increase the postspawning mortality rate of fish of larger size classes (Burton and Idler 1984; Rijnsdorp 1990; Burton and Maddock 1995). An additional ecological constraint could be related to the size of the time window for successful reproduction allowed by the environment (Cushing 1969). If this time window is shorter than the time needed to shed the successive batches of eggs, a further increase in egg production will not increase fitness. Although such a constraint may apply to the largest size classes, the fact that spawning duration is related to fish size suggests that the smaller size classes could in

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theory increase their reproductive investment and extend their spawning period. A morphological constraint is unlikely, since the maximum ovary weight in flatfish shows a large variation across related species and shows maximum values well above the gonadosomatic index observed in plaice (Rijnsdorp and Witthames 2005). It is also possible that individual genetic variation in reproductive investment was essentially exhausted by the 1960s and thus selection could no longer effect changes in investment (Gustafsson 1986; Price and Schluter 1991).

In conclusion, our study is inconclusive with regard to whether a fisheries-induced evolutionary increase in reproductive investment in plaice has occurred. No evidence for such an increase was obtained for the period 1960–2002, but the historic data on fecundity and ovary weight show an increase since the late 1940s. Although we cannot prove it, this change is consistent with a fisheries-induced change.

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Isolating the influence of growth rate on maturation patterns in the smallmouth bass (*Micropterus dolomieu*)[1]

Erin S. Dunlop, Brian J. Shuter, and Mark S. Ridgway

Abstract: In this study, we examine the divergence in growth and maturation between two populations of smallmouth bass (*Micropterus dolomieu*) introduced from a common source a century ago. To determine if the divergence in maturation is simply a plastic response to differences in growth rate, we use a new approach to estimate and then compare the probabilistic maturation reaction norms (PMRNs) for each population. The PMRNs for 5-year-old males are similar in the two populations, suggesting that the observed divergence in maturation is largely a plastic response to growth rate differences. For one population, we document the time course of maturation changes for the 60-year period from 1937 through 1990; while the mean length at maturation for 5-year-old males exhibits a steady downward trend (beginning at 31 cm and ending at 26 cm), their PMRNs vary over a much narrower range (25–27 cm) and do not exhibit a consistent temporal trend. These observations are consistent with the hypothesis that most of the observed change in maturation since introduction is a product of phenotypic plasticity, driven by environmentally based differences in growth rate. Our study provides an instructive example of how the PMRN approach can be used to isolate the role of growth rate variation in generating life history differences.

Résumé : Nous avons étudié la divergence dans la croissance et la maturation chez deux populations d'achigans à petite bouche (*Micropterus dolomieu*) introduites d'un même point d'origine il y a un siècle. Afin de déterminer si la divergence dans la maturation est simplement une réaction plastique à des différences de taux de croissance, nous avons utilisé une nouvelle méthodologie pour estimer et comparer les normes probabilistes de réaction (PMRN) de la maturation dans chaque population. La norme PMRN est semblable chez les mâles de 5 ans des deux populations, ce qui laisse croire que la divergence observée dans la maturation est en grande partie une réaction plastique aux différences de taux de croissance. Dans une des populations, nous avons tracé l'évolution chronologique des changements dans la maturation pour la période de 60 ans qui va de 1937 jusqu'aux années 1990; alors que la longueur moyenne à la maturité chez les mâles de 5 ans décline de façon constante (de 31 à 26 cm), leurs PMRN varient sur une gamme beaucoup plus étroite (25–27 cm) et ne montrent pas de tendance temporelle. Ces observations s'accordent avec l'hypothèse qui veut que la majeure partie du changement observé depuis l'empoissonnement est le résultat de la plasticité phénotypique, causée par des différences de taux de croissances reliés aux conditions environnementales. Notre étude fournit donc un exemple instructif de l'utilisation de la méthodologie PMRN pour circonscrire le rôle de la variation des taux de croissance dans la production de différences démographiques.

[Traduit par la Rédaction]

Introduction

Age at maturity, size at maturity, and growth rate are key life history traits that often vary among populations and are important to characterize because they influence population dynamics and resilience to overexploitation (Roff 1992; Heino and Godø 2002). Variation in life history traits among populations will reflect some combination of plastic and evolved responses to environmental and ecological differences. For example, differences in growth rate and matura-

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E.S. Dunlop.[2] Department of Zoology, University of Toronto, Toronto, ON M5S 3G5, Canada.
B.J. Shuter. Department of Zoology, University of Toronto, Toronto, ON M5S 3G5, Canada, and Harkness Laboratory of Fisheries Research, Aquatic Research and Development Section, Ontario Ministry of Natural Resources, 3rd Floor North, 300 Water Street, Peterborough, ON K9J 8M5, Canada.
M.S. Ridgway. Harkness Laboratory of Fisheries Research, Aquatic Research and Development Section, Ontario Ministry of Natural Resources, 3rd Floor North, 300 Water Street, Peterborough, ON K9J 8M5, Canada.

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[2]Corresponding author (e-mail: dunlop@zoo.utoronto.ca)

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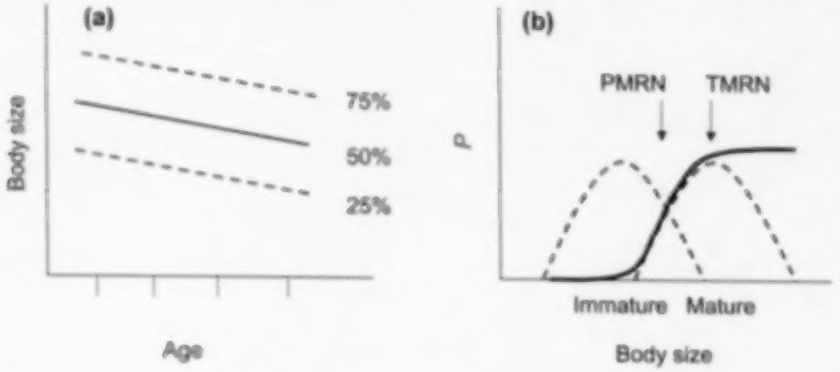
Fig. 1. Schematic diagram of the probabilistic maturation reaction norm (PMRN) concept. (*a*) The 25%, 50% (midpoint), and 75% probability positions of the PMRN. Note that the PMRN is shown as a continuous line, although position is calculated discretely for each age. (*b*) The body-size distributions (broken lines) of immature and newly mature individuals and the fitted logistic regression (solid curve) used to estimate the PMRN for a single age; *P* is the probability of maturing. The traditional maturation reaction norm (TMRN) is estimated as the mean size of newly mature individuals.



tion can result from a plastic response of the phenotype to changes in food availability, or, over time, may evolve in response to selective mortality (Law 2000; Hutchings 2004). Furthermore, recent research suggests that evolutionary responses can occur within just a decade in harvested populations (e.g., Olsen et al. 2005), much faster than was previously thought. A complete understanding of the processes that create life history variation requires knowledge of the relative contribution to the overall response of both phenotypic plasticity and evolved changes.

Unfortunately, it can be difficult to determine whether phenotypic changes in a population, or among populations, are plastic or evolved. Generally, common garden-rearing experiments or DNA analyses are used to test for evolved differences (e.g., Haugen and Vøllestad 2000; Koskinen et al. 2002); however, these methods can be expensive and are logistically difficult to use for species with long generation times. Therefore, in our study we chose to use maturation reaction norms (MRNs) as a tool to distinguish between phenotypic plasticity and changes that may be indicative of evolved responses.

The MRN for a population is the relationship between age at maturity and size at maturity for the individuals within the population. If individuals are part of a genetically distinct population but exhibit different growth rates because they vary in their experience of a specific environmental variable (e.g., food availability), the relationship between age and size at maturity expresses a classic reaction norm (Stearns and Koella 1986; Roff 2002; Ernande et al. 2004) (i.e., the systematic change in the expression of a phenotype in response to variation in a specific environmental variable (Schmalhausen 1949)). Abrams and Rowe (1996) and Abrams et al. (1996) investigated models in which the realized growth rate is determined, in part, by a behavioural or developmental trade-off between higher growth rate and greater mortality; age at maturity also changes adaptively in these models and, together with growth rate, determines size at maturity. Their analyses demonstrate that the optimal relation between age and size at maturity (i.e., the MRN) depends on which environment factor (e.g., food availability, predator abundance, temperature) drives variation in realized growth rate. Thus, a change in the MRN of a population over time may reflect a change in the genetic character of the individuals in the population (an evolved response), but it may also reflect a change of the environmental factor that is driving the variation in realized growth rate. Conversely, genetically distinct populations could in theory exhibit similar MRNs, but only if different environmental factors elicit identical MRNs from the different genomes involved. Although this is theoretically possible, the level of coincidence required for it to occur seems high enough to make it an unlikely event. In addition, common garden-rearing experiments (e.g., Reznick 1993; Haugen 2000) show that different MRNs evolve in genetically divergent populations. Thus, it seems reasonable that a comparison of population MRNs will lead to one of the following conclusions: (*i*) if two populations exhibit identical MRNs or if a single population exhibits no change in its MRN over time, the most parsimonious explanation is that there is no difference in the genetic traits that underlie the observed MRNs; (*ii*) a demonstration of differences, or changes, in MRNs raises the real possibility that evolved differences in genetic traits do exist; however, an assessment of the environmental sources of the observed variation in growth rates is required to confirm this.

A new method has been developed (Heino et al. 2002) to estimate MRNs probabilistically. Traditionally, a MRN was often estimated from the mean size of the maturing individuals in each age group (e.g., Reznick 1993). The estimator describes the relationship between growth rate and age–size at maturity and we will refer to it as the traditional estimator for the maturation reaction norm (TMRN). In contrast to the TMRN, the probabilistic estimator for the maturation reaction norm (the PMRN) is based on a direct estimate, for each age group, of the probability that an individual of a particular size will mature and requires information on immature individuals in the population (Fig. 1). A probabilistic descriptor of the maturation process is likely realistic in wild populations where maturation is often stochastic, owing to variable and complex environmental influences (Bernardo

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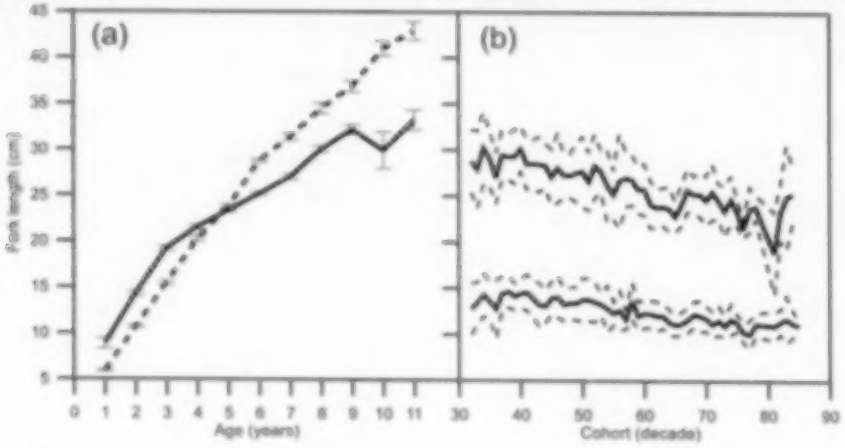
Fig. 2. (*a*) Size-at-age (mean ± 1 standard error) of smallmouth bass, using data collected in 1975–1985 in Opeongo Lake (broken line) and 1981–1982 in Provoking Lake (solid line). (*b*) Mean size (solid lines) ±1 standard deviation (broken lines around means) at age 2 (lower lines) and age 5 (upper lines) for Opeongo cohorts sampled during the creel survey of 1937–1990 (i.e., 30–90).



1993). Heino et al. (2002) have argued that (*i*) a probabilistic representation of the reaction norm is a more accurate depiction of how this trait is likely to be expressed in the wild; (*ii*) an estimator (i.e., the PMRN) that explicitly recognizes the probabilistic character of this trait will be unbiased in the face of changes in growth rate, while the TMRN will exhibit significant bias in the face of growth rate changes; (*iii*) thus, the PMRN should be used when attempting to isolate how the observed maturation schedule for a population is shaped by plastic responses to changes in growth rate.

Given that maturation in the wild is likely probabilistic, the following reasons are given for the interdependence of the TMRN on growth. First, maturation at young ages will often occur at small sizes if there are no individuals in the population with growth trajectories steep (i.e., fast) enough to intersect the upper bounds (i.e., the 75th percentile of the PMRN in Fig. 1*a*) of the MRN. Second, maturation at old ages will often occur at larger sizes if there are no individuals in the population with growth rates shallow (i.e., slow) enough to intersect the lower bounds (i.e., the 25th percentile of the PMRN in Fig. 1*a*) of the MRN. Consequently, the TMRN, estimated as the mean size at maturation for each age, could be biased low for young ages and biased high for old ages, depending on the individual growth rates in the population. If the average growth rates of a population change, the TMRN estimate may also change even though the actual MRN (and the PMRN) remain unchanged. To differentiate between changes in maturation that are due to growth (i.e., plastic responses) versus changes in maturation that reflect an evolutionary response, it is important to use a MRN estimator that does not vary with growth. In this paper we assess the above contentions by comparing the relative effectiveness of the TMRN and PMRN estimators in isolating the role played by growth rate variation in generating differences in the observed maturation schedules for two introduced populations of smallmouth bass (*Micropterus dolomieu*).

Our two study populations are from Provoking Lake and Opeongo Lake, located in Algonquin Provincial Park, Ontario. Smallmouth bass were introduced into each lake between 1900 and 1920 from the same source population (Christie 1957; Orendorff 1983). Since introduction, the populations have diverged in both their growth trajectories and their apparent maturation schedules: Provoking bass grow more slowly after age 5 (Fig. 2*a*) and have smaller sizes and younger ages at breeding than Opeongo bass (Orendorff 1983). Interlake-transfer experiments demonstrated that at least a portion of the growth reduction exhibited by the Provoking population is a plastic response to low food availability; however, the higher natural mortality rates suffered by Provoking adults (Orendorff 1983) may have produced an evolved response toward earlier maturation at smaller sizes (Reznick et al. 1990). In Opeongo, body sizes have undergone a declining trend since introduction (Fig. 2*b*) and maturation patterns may have changed accordingly. Since both populations have undergone considerable shifts in density and growth (Orendorff 1983; Shuter and Ridgway 2002), they provide ideal case studies for assessing the effectiveness of the PMRN estimator in identifying possible contributions of plastic and evolved changes to shifts in maturation patterns. In this study, we compare the current TMRN and PMRN for both populations, and we quantify temporal variation in the PMRN for the Opeongo population over the period 1937–1990. To date, the PMRN approach has been primarily used as a tool to examine temporal variation within populations (e.g., Grift et al. 2003; Olsen et al. 2004*a*) and we provide evidence that the approach can be used to study divergence between populations. PMRNs are being increasingly used to argue that evolution has occurred in harvested populations (e.g., Barot et al. 2004*b*; Olsen et al. 2005) and tests of their utility and robustness are required.

Methods

Background

Provoking and Opeongo are oligotrophic lakes located approximately 10 km apart. Provoking is considerably smaller than Opeongo (1.1 versus 58.6 km^2 in area) and supports just three fish species: smallmouth bass, yellow perch (*Perca*

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flavescens), and splake (*Salvelinus namaycush* × *Salvelinus fontinalis*). Opeongo contains numerous fish species including smallmouth bass, lake trout (*Salvelinus namaycush*), cyprinids (Cyprinidae), yellow perch, and pumpkinseed (*Lepomis gibbosus*).

There were three objectives to our study: (*i*) to describe the variation in growth rates of breeding males within the two populations and document the divergence in growth rates and maturation between them; (*ii*) to estimate and compare the current position of both the TMRN and the PMRN for each population; and (*iii*) to estimate temporal variation in the TMRN and PMRN for the Opeongo population. Data from three different field surveys were used to meet these objectives: (*i*) breeding-male surveys conducted from 1993 to 2003 on Opeongo and from 2000 to 2003 on Provoking; (*ii*) direct population sampling conducted from 2000 to 2002 on both lakes; and (*iii*) harvest sampling from an annual creel survey that has been conducted on Opeongo since 1936.

Breeding-male surveys

Smallmouth bass display paternal care in the form of an extended nest-guarding period in the spring and early summer. A long-term study of Opeongo guarding males has been conducted from 1980 to the present (Shuter et al. 1980; Ridgway et al. 1991). The study site for this work (Jones Bay) is located in the south arm of Opeongo, has a perimeter of 5 km, and is divided into three sections: south, central, and north. The study involves monitoring smallmouth bass nests frequently throughout the nesting period. Male nest-guarders are captured, measured, marked with tags, and released back onto their nests within 1–5 min of first capture. Body length of male nest-guarders is measured and 3–6 scales are removed for aging purposes. From 1993 to 1997, all the nesting males in all sections of Jones Bay were captured, measured, and released. From 1998 to 2003, all the nesting males in the south section and all previously tagged males in the central and north sections of Jones Bay were sampled. From 1993 to 2003, all nesting males were tagged with external T-bar tags (Hallprint, Victor Harbour, South Australia) placed beneath the soft dorsal fin and were given dorsal-spine clips. From 1997 to 2003, all nesting males were also tagged with internal passive integrated transponder (PIT) tags (Biomark, Boise, Idaho) placed in the cheek. Dorsal-spine clips are permanent and can be used to determine which fish have been tagged previously. Individual smallmouth bass that spawn repeatedly show high nest-site fidelity, with 94% of experienced males returning to within 200 m and 35% of experienced males returning to within 20 m (the modal distance category) of their previous nest site (Ridgway et al. 2002). Therefore, from 1993 to 2003, it was possible to determine which males were likely first-time nesters (males without clips) and which males had nested in a previous year (those with clips). As the rate of PIT-tag loss was low (M. Ridgway, unpublished data), it was also possible to identify most individual males in each year that they nested.

A similar survey of nesting males was conducted on Provoking from 2000 to 2003. The entire shoreline of Provoking was monitored frequently by snorkelers throughout the nesting period to locate smallmouth bass nests and capture males. All males that were identified (by the presence of easily visible dorsal-spine clips and (or) external T-bar tags) as nesters from a previous year were captured, sampled again, and released back onto their nests. Smallmouth bass nest in specific concentrated areas on Provoking (Orendorff 1983) and it is possible to sample most nesting males in these concentrated areas. Return rates for males nesting on Provoking are low for all ages (mean return rate 10%), and therefore most males sampled that were not captured in a previous year (as identified by clips) were most likely first-time nesters.

Direct population sampling and creel-survey sampling

Direct population sampling was conducted on Provoking and Opeongo in the late summer (September) of 2000, spring (May) of 2001, and late summer (end of August to early September) of 2002. Trap-netting (24-h sets), minnow trapping (24-h sets), and angling were used to capture individuals. For all captured smallmouth bass, fork length was measured, scale samples were taken for aging and back-calculation, sex was recorded, and the state of maturity was assessed by internal examination.

Sampling of the angler harvest on Opeongo was carried out through a point-access creel survey that has been run annually on the lake since 1936 (for details see Shuter et al. 1987). Harvested fish were examined by survey staff, scale samples for aging and growth back-calculation were taken, and fork length, weight, sex, maturity status, and data on diet were recorded. Annual sample sizes typically exceeded 100 fish.

Reconstructing individual growth histories

The individual growth history of each captured nesting male was reconstructed by back-calculating its fork length at each age from the distance to each annulus identified on its scale sample (Francis 1990). The aging and back-calculation techniques were validated using tagged, recaptured Opeongo smallmouth bass sampled over a decade, as well as multiple aging structures (scales, spines, opercula) from both populations. The same back-calculation techniques were used to estimate individual growth histories for 4-, 5-, and 6-year-old fish sampled during the creel survey. Scale samples from at least 40 fish from each cohort born over the period 1932–1985 were processed in this way. Multivariate analysis of variance (MANOVA) was used to test between-lake differences in growth histories (i.e., size at age) for each age at first nesting and within-lake differences in growth histories among ages at first nesting.

Estimation of age and size at breeding

Males captured on nests were used to give direct estimates of age and size at breeding. The age and length distributions of first-time nesting males sampled in 2001–2003 were compared between populations using analysis of variance (ANOVA). Those years were selected because 2000 was the first year of tagging in Provoking and recaptures could therefore be identified in 2001. The mean size of first-time nesting males at each age was also estimated by cohort, and between-lake differences among pooled cohorts were tested using ANOVA.

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Estimation of TMRNs and PMRNs

The TMRN for a particular age is estimated as the mean size of individuals breeding for the first time at that age. The procedure for estimating a PMRN is considerably more complex because it requires a representative sample of body sizes for both the newly mature and the immature fish in each of the age groups to be included in the PMRN. Logistic regression is then applied to the data for each age group to estimate the length at which the probability of maturing is 50% (Fig. 1). These estimated sizes form the age-specific midpoints of the PMRN, and other percentiles (e.g., 25%, 75%) can also be estimated (Fig. 1). In our analyses of the Opeongo and Provoking data, we could only develop reliable estimates for the PMRN of age-5 males because (*i*) the number of younger males that mature in either population is so small that we were unable to collect sufficient data to obtain reliable PMRN estimates for those age groups, and (*ii*) for older males, it was impossible for us to reliably distinguish between newly mature fish and fish that had matured in previous years.

For the direct population sampling in Opeongo in the late summer of 2000 and 2002, and for the creel-survey sampling from 1937 to 1990, we assumed that the 5-year-old males that were classified as mature fell into one of two categories: (1) those that had reproduced for the first time at age 5 in the spring of their year of capture, and (2) those that were preparing to reproduce for the first time at age 6 in the spring following their year of capture. To construct the PMRN for 5-year-olds, we needed to remove the males of category 2 from the estimate. This was done by using a discriminant function to separate category 1 and 2 fish, based on their growth histories. The discriminant function was based on the back-calculated growth histories (ages 1–4) of two groups of nesting males sampled from the 1991–1998 cohorts in Opeongo: group 1 included just those fish known to have spawned for the first time at age 5 and group 2 included just those fish known to have spawned for the first time at age 6. The discriminant function was developed using the relative change in body length (R_i) for age groups 1–4, calculated as follows:

$$R_i = \frac{\Delta F_i - \overline{\Delta F_i}}{S_i}$$

where ΔF_i is the change in fork length from age i to age $i + 1$, $\overline{\Delta F_i}$ is the mean change in fork length from age i to age $i + 1$, and S_i is the standard deviation of the change in fork length from age i to age $i + 1$. R_i rather than ΔF_i values were used in the discriminant function to allow for extraneous differences in body size that might exist between populations and through time. The discriminant function was constructed to identify membership in group 1 or group 2 based on values for R_1, R_2, R_3, and R_4. The discrimination was significant ($F_{[4,258]} = 21.7$, $P < 0.0001$, $N = 263$; correct classification 73%). This function was applied to the R_i values calculated for all mature age-5 males collected from either the late-summer direct population samples or the creel survey, in order to classify these fish into one of the two categories defined above: category 1 males were those that had spawned for the first time at age 5 in the spring of their year of capture, and category 2 males were those that would spawn for the first time at age 6 in the spring following their year of capture.

To estimate the PMRN for age-5 males, the size distribution of both immature and newly mature 5-year-old males is required. The size distribution of maturing 5-year-olds was derived by pooling (*i*) the back-calculated lengths at age 5 for all category 1 males identified by the discriminant analysis; (*ii*) observed late-summer and fall lengths of 4-year-old males that had developed mature gonads — since very few individuals spawn at age 4, we assumed that these fish were preparing to spawn for the first time at age 5; and (*iii*) observed spring lengths of 5-year-old males that had developed mature gonads. The size distribution of immature fish was derived by pooling (*i*) the back-calculated lengths at age 5 for all category 2 males identified by the discriminant analysis; (*ii*) observed late-summer and fall lengths of 4-year-old males that did not exhibit any gonadal development; and (*iii*) observed spring lengths of 5-year-old males that did not exhibit any gonadal development. The same procedure, using the Opeongo discriminator, was applied to the Provoking males taken during the direct sampling of that lake over the period 2000–2002. The PMRN for 5-year-old males was then estimated for each population by running a simple logistic regression on the length data from these representative samples of immature and newly matured individuals. The logistic regression was used to estimate the size at which the probability of maturing was 25%, 50%, and 75%. The significance of each logistic regression was tested using a χ^2 test.

In the case of the creel-survey estimates, individuals were pooled by decade in which they were born and the 1930s and 1940s cohorts were combined to obtain adequate sample sizes. A generalized linear model using a log-likelihood ratio test (McCullagh and Nelder 1989) was used to test for between-lake differences in the 2000–2002 PMRNs and for temporal changes in the Opeongo PMRNs from the cohorts of the 1930s to the 1980s.

TMRNs were estimated for 5-year-old males in both populations using the direct population sampling in 2000–2002. A time series of TMRN estimates was obtained for the Opeongo population using data from creel-sampled males captured over the period 1937–1990 (TMRN estimated by decade of birth as was done for the PMRN). For both cases, the TMRN was estimated as the mean size of newly mature 5-year-old males, and differences between lakes and within Opeongo were tested using ANOVA. All statistical tests were done in STATISTICA® (version 6.1; Statsoft Inc. 2003).

Results

Variation in individual growth rates within and between populations

In both populations, the faster growing members of a cohort breeded first. This difference was clearly evident for the 1995 Opeongo cohort (Fig. 3; MANOVA for growth rates through age 4 compared across groups that breed first at ages 4–8: $F_{[4,10]} = 257.3$, $P < 0.001$, $N = 92$) and was typical of other Opeongo cohorts. In Provoking, those that nested at early ages (e.g., age 5) had higher growth rates (Fig. 3); however, the difference among all ages was not significant (MANOVA: $F_{[4,12]} = 0.8$, $P > 0.5$, $N = 56$). Also, Opeongo

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Fig. 3. Size-at-age (mean ± 1 standard error) of first-time nesting male smallmouth bass from the 1995 cohort in Opeongo (*a*) and Provoking (*b*). The shaded area in *b* represents the range from Opeongo shown in *a*. Each symbol represents the growth history for a different age at first nesting.

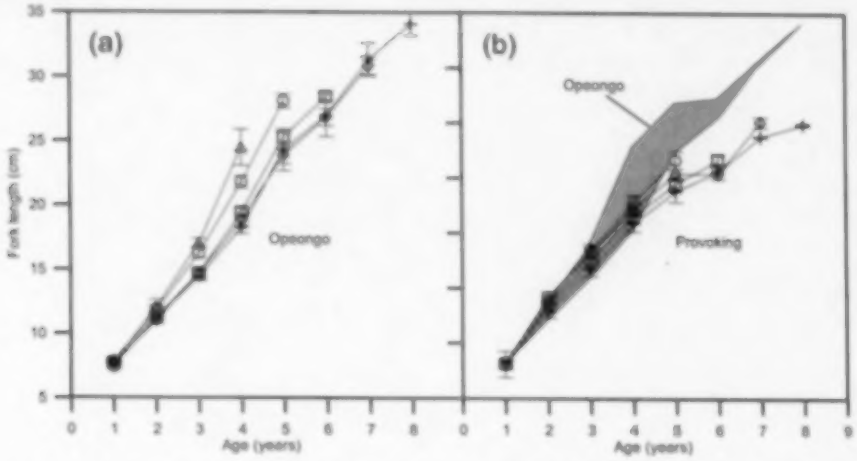
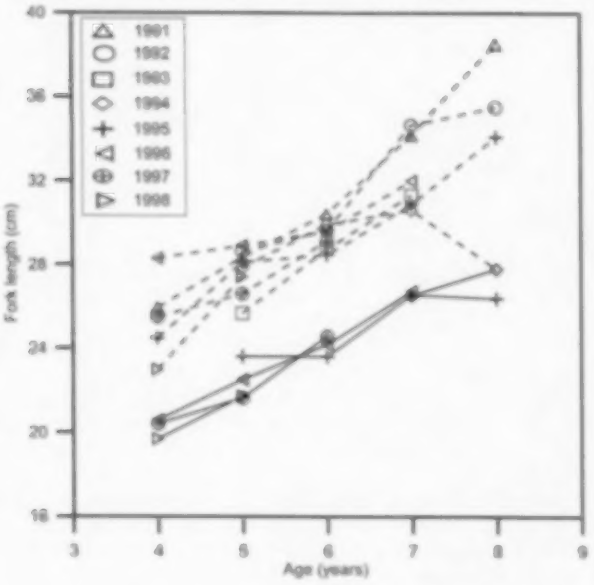


Fig. 4. Mean size of first-time nesting males by age for the 1991–1998 cohorts in Provoking (solid lines) and Opeongo (broken lines). Each symbol represents a different cohort.



nesting males had significantly higher growth rates than Provoking males at ages 5–7 (Fig. 3; MANOVA, age 5: $F_{[5,33]} = 14.4$; age 6: $F_{[8,55]} = 31.2$; age 7: $F_{[7,33]} = 15.5$; $P < 0.001$, $N = 142$). Although growth rates at age 8 were higher for Opeongo than for Provoking, sample sizes were likely too small for statistical significance (MANOVA: $F_{[3,1]} = 14.0$, $P = 0.19$, $N = 5$).

Variation in age and size at breeding between populations

Provoking nesting males had smaller sizes both before (ANOVA: $F_{[1,458]} = 327.0$, $P < 0.01$, $N = 460$; 24.6 ± 3.6 cm (mean ± SD) for Provoking and 32.3 ± 5.0 cm for Opeongo) and after (ANOVA: $F_{[1,306]} = 174.4$, $P < 0.01$, $N = 308$; 24.0 ± 3.3 cm for Provoking and 29.1 ± 3.4 cm for Opeongo) removal of experienced nesters (i.e., recaptures from a previous year) relative to those in Opeongo. Before experienced nesters were removed from the analysis, Provoking males nested at significantly younger ages than Opeongo males (ANOVA: $F_{[1,458]} = 29.7$, $P < 0.001$, $N = 460$; 6.0 ± 1.4 years for Provoking and 7.0 ± 1.6 years for Opeongo). However, after experienced nesters were removed, the age distribution of first-time nesting males was not significantly different between populations (ANOVA: $F_{[1,306]} = 0.3$, $P > 0.5$, $N = 308$; 6.0 ± 1.3 years for Provoking and 6.0 ± 1.0 years for Opeongo). The mean size of first-time nesting males was significantly greater in Opeongo than in Provoking across all ages and cohorts (Fig. 4; ANOVA: $F_{[1,517]} = 237.0$, $P < 0.001$, $N = 519$).

Variation in TMRNs and PMRNs between populations and within Opeongo

The strong association between rapid growth prior to maturation and early maturation (Fig. 3) was the basis for the discriminant function that we used to construct the mature and immature size distributions needed for our PMRN estimates. The effectiveness of this discriminant function in accurately identifying males that were maturing for the first time at age 5 was demonstrated by the fact that the mean size of males identified by the function from the direct population samples in 2000–2002 was similar to the mean size of 5-year-old first-time spawners in both populations (26 versus 27 cm in Opeongo; 23 versus 22 cm in Provoking).

The TMRNs (i.e., the mean sizes at maturation derived from the 2000–2002 direct population sampling) differed between the populations but the PMRNs were similar. As was observed for nesting males, the mean size of newly mature males (TMRN) was significantly greater in Opeongo than in Provoking (Fig. 5; Table 1). The logistic regressions used to estimate the age-5 PMRNs for 2000–2002 were significant ($P < 0.01$) for both populations (Table 1); however, the posi-

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tions of these PMRNs did not differ (Fig. 5; log-likelihood test: log likelihood = −42.5, $P > 0.50$). The sample sizes used for the PMRN estimates were fairly low for both populations (Table 1), and this reduces their precision (Barot et al. 2004*a*); however, both logistic curves provided visually good fits to the data, were statistically significant, and were essentially identical for the two populations (Fig. 5).

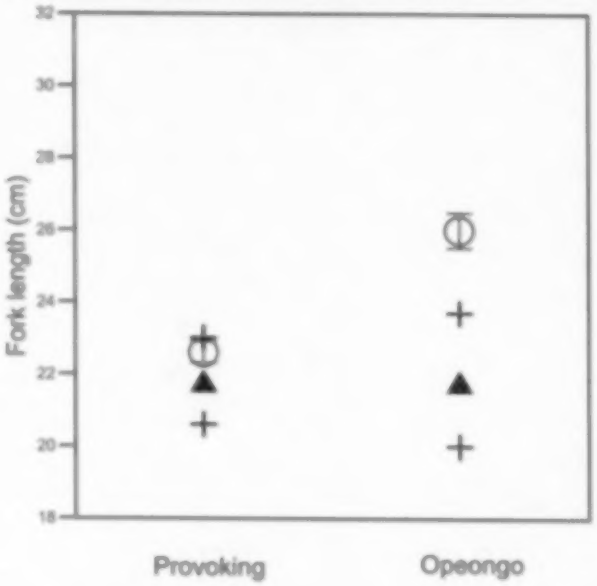
The TMRN for 5-year-old males derived from the Opeongo creel survey showed a consistent and significant (ANOVA: $F_{[5,175]} = 27.0$, $P < 0.001$) trend through time. It decreased dramatically from the 1930s to the 1950s cohorts and then stabilized for the 1960s to the 1980s cohorts (Fig. 6). The logistic regression used to estimate the position of the Opeongo PMRNs from the creel survey data was significant for all pooled cohorts (Table 1). The PMRN estimate decreased from the 1930s to the 1950s and then increased from the 1960s to the 1980s but the overall change was not as large as that observed in the TMRN (Fig. 6). There was a significant cohort effect, indicating that differences in the position of the PMRN over time were significant (log-likelihood test; log likelihood = −272.5, $P < 0.001$). The TMRNs for the early cohorts lie above the 75th percentile of the PMRNs, but they tend to fall within the 25th and 75th percentiles for the more recent cohorts.

It should be noted that (*i*) the 2000–2002 PMRNs were derived from a direct population sampling program that employed a range of gear designed to provide representative samples of the size distributions of all 4- and 5-year-old fish in both lakes, and (*ii*) the Opeongo PMRN time series was derived from samples taken by a size-selective angling fishery. Although Shuter et al. (1987) found no evidence of changes in the size selectivity of 5-year-olds over the life of the creel survey, the harvest of 4-year-olds and, to a lesser degree, 5-year-olds was biased toward larger fish. Since immature 5-year-olds tend to be smaller than maturing 5-year-olds (Fig. 3), size-selective sampling will produce a positive bias in the estimated size distribution for immature 5-year-olds, shifting it toward larger sizes and this will cause the Opeongo creel-based PMRNs to overestimate the true PMRNs by a small but relatively consistent amount. Thus, the creel-based time series of Opeongo PMRN estimates (Fig. 6) cannot be directly compared with the 2000–2002 PMRN estimate (Fig. 5) derived from the direct sampling program. However, although the creel-based estimates may be biased toward large sizes, the temporal changes in the PMRN (Fig. 6) are relative and therefore readily interpretable.

Discussion

The analysis of changes in the MRN can help identify whether observed differences in maturation schedules are likely the product of evolved or plastic responses to ecological differences: temporal stability in the MRN suggests that the observed differences are largely the product of plastic responses; systematic change in the MRN raises the possibility that the observed differences may be the product of evolved responses (Heino 2002; Ernande et al. 2004; Stearns and Koella 1986). Downward trends in the MRN (and shifts to younger, smaller breeders) have been documented in commercial fish populations (Grift et al. 2003; Olsen et al. 2005) and suggest evolved responses to harvest; such trends will

Fig. 5. The TMRN (mean ± 1 standard error) (○) and midpoint of the PMRN (▲) for Provoking and Opeongo age-5 males captured in 2000–2002. The plus signs (+) represent the 25th (lower) and 75th (upper) percentiles of the PMRNs.



likely cause a reduction in body sizes in the catch and a decline in the quality of the fishery (Ernande et al. 2004). Moreover, evolved responses may be difficult to reverse (Law 2000) and it is therefore important for managers to detect such responses as soon as possible so that they can act to ameliorate them. This requires effective procedures for estimating the MRN.

Traditional estimation of the MRN (e.g., the TMRN) was often done by plotting the relationship between age and size at maturity without considering data on immature individuals (e.g., McKenzie et al. 1983; Reznick 1990). However, an explicitly probabilistic estimator (the PMRN) should be superior to the TMRN because the position of the TMRN will be strongly affected by the mean somatic growth rate characteristic of the population (Heino et al. 2002). Our comparison of TMRN and PMRN estimates of the Provoking and Opeongo MRNs provides a strong confirmation of this assertion: the PMRN estimates were unresponsive to both the growth rate difference between Opeongo and Provoking fish and the temporal shift in the growth rates of Opeongo fish; the TMRN estimates varied directly with these growth rate changes – lower growth rates were always associated with lower TMRN values. As Heino et al. (2002) highlight, this is a necessary consequence of the inherently probabilistic character of the MRN. Given that (*i*) there is an age-specific range of sizes over which maturation can occur, and (*ii*) the probability of maturing increases from zero at the lower bound of the range to 1 at the upper bound, then, when the mean growth rate is low, only a few fish can reach the lower end of the maturation size range and thus the TMRN estimate derived from the small fraction of those fish that do mature will sit near the lower bound of the maturation size range. In contrast, when the mean growth rate is high, most

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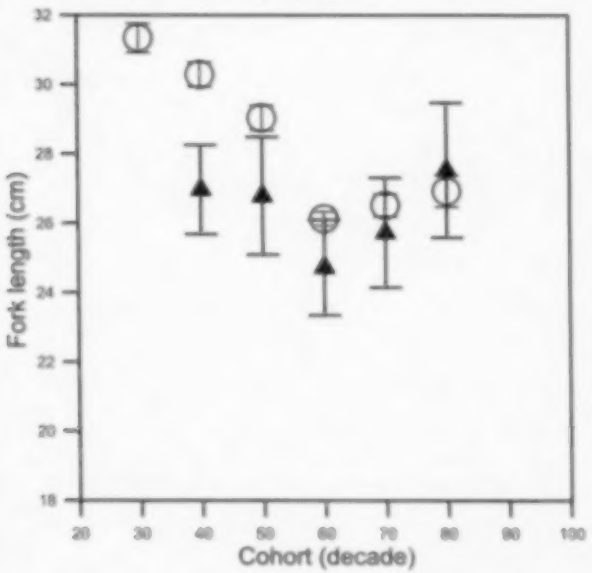
Table 1. Results of the logistic regressions used to estimate the probabilistic maturation reaction norms (PMRN) for Provoking Lake and Opeongo Lake cohorts of smallmouth bass (*Micropterus dolomieu*) sampled in 2000–2002 (1990s) and from the creel survey (1930s to 1980s).

		Reaction norm		Body size (cm)			
				Immature		Newly mature	
Population and cohort	*N*	χ^2	*P*	Mean	SE	Mean	SE
Provoking							
1990s	62	12.3	<0.001	21.1	0.22	22.6	0.29
Opeongo							
1990s	34	10.4	<0.01	22.4	0.90	26.0	0.49
1980s	79	21.6	<0.00001	23.7	0.32	26.9	0.46
1970s	147	69.0	<0.00001	22.2	0.25	26.5	0.33
1960s	304	160	<0.00001	22.4	0.15	26.1	0.20
1950s	84	48.3	<0.00001	24.1	0.50	29.0	0.35
1930s to 1940s	94	38.7	<0.00001	26.6	0.53	30.5	0.29

Note: Sample sizes (*N*) used in estimating the PMRNs and results of the χ^2 analysis (χ^2 and *P* value) used to test for significance of the logistic regressions are shown. The mean size and standard error (SE) are shown for immature and newly mature 5-year-old males used in estimating the PMRNs.

Fig. 6. The TMRN (mean ± 1 standard error) (○) and the midpoint of the PMRN (▲) for 5-year-old males in the 1930–1980 (i.e., 30–80) cohorts in Opeongo measured from the creel survey. The vertical bars above and below the solid triangles indicate the 75th and 25th percentiles, respectively.



fish will reach the upper end of the maturation size range and the TMRN estimate derived from the large fraction of those fish that do mature will sit near the upper bound of the maturation size range. Hence, the TMRN must vary with growth rate even when the MRN (and its PMRN estimate) remains unaltered.

Our study illustrates the usefulness of mark–recapture data in MRN research. The mark–recapture data permitted us to differentiate newly matured males from previously matured males and thus show that a large and significant difference in the age distributions of all the breeding males in Opeongo (older) and Provoking (younger) disappeared when experienced spawners (i.e., recaptures) were removed from both age distributions. Thus, we could conclude that the initial difference in age distributions was largely driven by the higher mortality rate in Provoking (Orendorff 1983) rather than by a difference in maturity schedules. Since experienced spawners have endured the growth and mortality costs of reproduction for varying periods of time, their contribution to the overall size and age distribution of mature fish will cause these distributions to reflect an ill-defined mixture of both the maturation schedule of the population (the primary focus of an MRN study) and the post-maturation growth and mortality rates suffered by mature individuals. Hence, in an MRN study, it is always desirable to identify and separate first-time breeders from experienced breeders. In situations where experienced adults cannot be identified and separated from inexperienced ones, alternative approaches to PMRN estimation based on maturity ogives have been proposed by Barot et al. (2004*a*) but they suffer from some potentially limiting assumptions when data on mortality are lacking.

In fishery science, two common indices used to describe maturation patterns are age and size at 50% maturity (e.g., Gangl and Pereira 2003; Olsen et al. 2004*b*). These measures involve running a logistic regression using either age or size as the predictor variable and maturation status as the binary response variable and are commonly referred to as maturity ogives. The maturity ogives can be used to estimate the length or age at which 50% of the population is mature. This is distinct from the PMRN estimates, which determine the body size at which the probability of becoming mature is 50%. PMRN estimates are superior to maturity ogive estimates for two reasons: (*i*) they summarize maturation patterns in a single descriptor rather than requiring two separate estimates for age and size, and (*ii*) they are not subject to the growth and survival costs incurred during and after the reproductive event itself. The main distinction is that the maturity-ogive estimate includes data from individuals that have matured at previous ages (i.e., includes experienced breeders) and is thus subject to the same bias caused by mortality that we see in the TMRN estimate. This is substantiated by the smaller size at 50% maturity (calculated using

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the direct population sampling in 2000) for Provoking versus Opeongo males (22 versus 24 cm) and females (21 versus 26 cm). The between-lake differences in maturity ogives, unlike those in the PMRNs, are significant (at a 5% level using a log-likelihood ratio test) and correspond to the direction of growth rate patterns observed in the two populations.

For the Opeongo population, temporal variation in our time series of TMRN values differed significantly from the variation exhibited by our PMRN values: the TMRN values declined progressively over a 5-cm range, while the PMRN values varied erratically over a 2-cm range. These patterns of variation were accompanied by a general decline in the mean somatic growth rate of the population and a pattern of abundance variation characteristic of an introduced population — abundance rose rapidly, peaked, and then contracted somewhat and appeared to stabilize (Shuter and Ridgway 2002). The relative stability of the PMRN values suggests that the observed changes in the Opeongo maturation patterns were largely plastic responses to growth rate changes. This finding contrasts with recent work on North Sea plaice, *Pleuronectes platessa* (Grift et al. 2003) and northern cod, *Gadus morhua* (Olsen et al. 2004*a*), where strong downward trends in PMRN values were observed and interpreted as reflecting evolved responses to high fishing-mortality rates. The absence of such trends in the Opeongo time series could reflect the lower fishing-mortality rates experienced by this population (Shuter et al. 1987) than by the marine populations studied to date.

Our comparison of Opeongo and Provoking MRNs also suggests that the observed differences in maturity schedules between these populations was largely a plastic response to differences in growth rate: both growth rate and TMRN estimates for Provoking were significantly lower than those for Opeongo; however, the PMRN values for the two populations were essentially identical. In environments with highly size-selective mortality of adults, evolution favours those that mature earlier at smaller sizes (e.g., Reznick et al. 1990). Although natural mortality rates of adults are higher in Provoking than in Opeongo (Orendorff 1983), their ages at maturation are similar and, at least for 5-year-olds, their PMRN values are very similar. The interpopulation difference in growth rate, which seems to be driving the maturity difference, seems itself to be a plastic response to a difference in food availability (Orendorff 1983). This is strongly suggested by the results from a 1982 experiment where smallmouth bass transferred from Provoking to a lake supporting a low-density, high-growth smallmouth bass population increased their growth rates, while bass transferred from the high-growth population to Provoking decreased their growth rates (Orendorff 1983).

The PMRN approach to disentangling plastic from evolved responses that we present here assumes that variation in growth is environmentally based (Bernardo 1993) and caused by the same factors (i.e., fast-growing individuals in one population grow fast for the same reason as individuals in the other population) (Abrams and Rowe 1996). This may not always be the case because growth rates themselves can evolve (Conover and Munch 2002) and individuals may exhibit different relations between growth and age–size at maturity, depending on the kind of environmental factor that drives variation in growth (Abrams and Rowe 1996). However, our overall conclusion (i.e., differences in maturation between bass in Provoking and Opeongo are the result of phenotypic plasticity) seems reasonable because (*i*) growth rates in these populations have a significant and common food-driven component as suggested by a transplant experiment where Provoking bass increased their growth when transplanted to a low-density population and fast-growing bass transplanted to Provoking decreased their growth (Orendorff 1983); and (*ii*) the lack of a clear temporal trend in Opeongo PMRNs and the similar position of the PMRNs between Provoking and Opeongo suggests that there has been no underlying change in other factors (e.g., growth evolution and behaviour) that may influence maturation.

There are a growing number of studies utilizing PMRNs to argue that evolution has occurred in commercially important fish populations (e.g., Barot et al. 2004*b*; Olsen et al. 2005) and tests of the PMRN approach, such as the one we present here, are needed. To date, PMRNs have been used primarily to study temporal changes in maturation within harvested populations (e.g., Grift et al. 2003; Olsen et al. 2004*a*). Our study demonstrates how PMRNs can be used to isolate the influence of growth on maturation when characterizing divergence between populations in response to ecological differences.

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Life history and ecological correlates of extinction risk in European freshwater fishes[1]

John D. Reynolds, Thomas J. Webb, and Lorraine A. Hawkins

Abstract: We used phylogenetically based comparative analyses to test for associations between extinction risk in European freshwater fishes and a variety of life history, ecological, and biogeographical traits. Based on the World Conservation Union classification scheme, a total of 47% of Europe's 287 native species are classified as threatened with extinction. Threatened species are significantly smaller than less-threatened species in the same genera when analyses are restricted to fully freshwater species. This trend is reversed when anadromous genera are included. These comprise many large-bodied species in which fishing has often played a greater role in declines than in other taxa. Threatened species did not differ significantly in their habitats, although they tended to occupy a narrower variety of habitats biased toward streams and rivers. Threatened species occupy much narrower latitudinal ranges than close relatives that are less threatened, and they also have more southerly distributions where pressures on habitats are intense. This study suggests that links between life histories and threat status of freshwater fishes are not as clearcut as for marine species. For fish restricted entirely to freshwater, small-bodied species are most at risk owing to their naturally small ranges, which may put them in a more precarious position when their habitats are impacted by humans.

Résumé : Nous avons utilisé des analyses comparatives de nature phylogénitique pour évaluer chez les poissons d'eau douce d'Europe les associations entre le risque d'extinction et une variété de caractéristiques démographiques, écologiques et biogéographiques. D'après le schéma de classification de l'Union mondiale pour la nature, 47 % des 287 espèces indigènes de poissons d'Europe sont menacées d'extinction. Dans un même genre, les espèces menacées ont une taille significativement inférieure à celle des espèces moins menacées, lorsque l'analyse ne considère que les espèces franchement dulcicoles. La tendance est inversée si on inclut les genres anadromes; ceux-ci comprennent plusieurs espèces de grande taille corporelle, chez lesquelles la pêche a joué un rôle plus important dans le déclin que chez les autres taxons. Les espèces menacées ne diffèrent pas significativement par leurs habitats, bien qu'elles aient tendance à occuper une gamme plus étroite d'habitats, surtout concentrée dans les ruisseaux et les rivières. Les espèces menacées occupent des aires de répartition en latitude plus étroites que les espèces proches moins menacées et elles ont aussi des répartitions plus australes dans lesquelles les pressions sur les habitats sont intenses. Notre étude indique que les liens entre le cycle biologique et le statut de vulnérabilité de l'espèce ne sont pas aussi clairs que chez les espèces marines. Chez les poissons entièrement restreints aux eaux douces, les espèces de petite taille corporelle sont plus à risque à cause de leurs répartitions naturellement plus restreintes, ce qui peut les placer dans une situation plus précaire lorsque leurs habitats subissent l'impact des activités humaines.

[Traduit par la Rédaction]

Introduction

Freshwater fish species face severe threats in many parts of the world. The main problems include physical alteration of habitats, introduction of alien species, pollution, and fishing (Miller et al. 1989; Leidy and Moyle 1998; Harrison and Stiassny 1999). It is not yet possible to say with any confidence what percentage of the world's fish species are threatened with extinction because the global assessments by the World Conservation Union (IUCN 2003) have considered only approximately 5% of the 28 000 fish species that have been described. When analyses are restricted to the 20 countries for which assessments are most complete, 17% of freshwater fish species are considered threatened (IUCN 2003). This new estimate matches the suggestion by Leidy and Moyle (1998) that more than 20% of species may be at risk

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J.D. Reynolds.[2] Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK.
T.J. Webb. Environment Department, University of York, Heslington, York YO10 5DD, UK.
L.A. Hawkins. Gatty Marine Laboratory School of Biology, University of St Andrews, Fyfe, KY16 8BL, Scotland.

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[2]Corresponding author (e-mail: reynolds@uea.ac.uk).

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of extinction. The comparable figures for birds and mammals are 12% and 24%, respectively (IUCN 2003). These assessments confirm the consensus that freshwater fishes are facing severe threats globally (Bruton 1995; Harrison and Stiassny 1999; Duncan and Lockwood 2001).

The paucity of information about the status and ecology of fishes, compared, for example, with information from the world's birds and mammals, has seriously hampered efforts to assess conservation status and manage populations accordingly. Distributions and ecological requirements are often poorly known, and population trends are rarely available (except for commercially important species).

It may be possible to predict the conservation status of fishes by examining life history and ecological correlates of extinction risk (Reynolds et al. 2001*a*). There have been several attempts to do this for marine species that are subject to fisheries (Jennings et al. 1998; Rochet 2000; Dulvy and Reynolds 2002). Most of these studies have found correlations between the extent of population decline under fishing pressure and one or more life history traits such as body size and age at maturity. These findings support theoretical predictions that "fast" life histories, including associated traits such as rapid growth and maturity, should be related to the ability of populations to withstand fisheries (Rochet 2000; Reynolds et al. 2001*b*; Reynolds 2003).

It is more difficult to make predictions about links between life histories and conservation status of freshwater fishes. This is because unlike most commercially important marine fishes where there is a single overriding threat (direct mortality by fisheries), freshwater fishes often face a greater range of threats. The effects of this variety of threats on species with various types of life history cannot be predicted easily (Duncan and Lockwood 2001). For example, if small-bodied species tend to occur in heavily impacted habitats, small size and associated fast life history traits would be correlated with extinction risk. This would reverse the predicted relationships between life histories and population status compared with those found in marine species. Indeed, a study of freshwater fishes in Virginia found no overall association between body size and vulnerability to extinction and a tendency of small-bodied minnows (Cyprinidae) to be more extinction prone (Angermeier 1995). Parent and Schriml (1995) also found no overall association between body size and risk status of fishes in the Great Lakes – St. Lawrence drainage of North America, although species with late ages at maturity tended to be under greater threat. This study found relationships between risk of extinction and characteristics of habitats. In contrast with the two studies above, Froese and Torres (1999) reported a weak association between large body size and threat status of freshwater species based on the IUCN's Red List (IUCN 1996).

The conflicting results of studies of freshwater fishes may stem from regional differences in the nature of threats as well as differences in methodology. Ambitious analyses such as the study by Froese and Torres (1999) provide wide spatial coverage at the expense of highly uneven taxonomic and geographical sampling. An important issue in taxonomic sampling and analyses involves the treatment of individual species as separate data points (Harvey and Pagel 1991; Reynolds et al. 2001*a*). Related species share many aspects of life histories and ecology as a result of inheritance from common ancestors rather than as the result of independent evolutionary events. Caution is therefore required in any analysis that attempts to treat them as independent data points.

In this study, we provide the first analyses of relationships between threat status, life histories, and ecology of native European fishes. The conservation status of nearly all of the native species has been assessed in this region (Lelek 1980; Maitland 2000; IUCN 2003), and a reasonable amount of information is available concerning key life history traits and habitat characteristics. Most of our analyses use methods that make explicit use of evolutionary relationships among taxa. This method thereby yields comparisons that are more robust statistically than traditional cross-species comparisons. Furthermore, by comparing differences among species within lineages, we control for many potentially spurious differences that can arise when distantly related taxa are combined in cross-species analyses.

Materials and methods

Taxonomic and geographic scope

We compiled a database of life histories, ecology, and conservation status of native European freshwater fishes. The region corresponds to that used by Maitland (2000) bordered by the Arctic and Atlantic oceans and the Mediterranean and Black seas and extending east to the Caucasus Mountains, the Caspian Sea, and the Ural Mountains. We considered all native fish species that spend a significant part of their life cycle in fresh water based on descriptions by Maitland (2000). We include anadromous species but analyse the data both with and without them. We exclude 29 nonnative species as well as borderline cases involving fish that primarily occupy marine habitats but also occasionally enter brackish waters or the lower reaches of waters that enter the sea. These criteria yield a total of 316 species for an overall assessment of threat status. We then focus on 138 species that could be paired between close relatives that differed in threat status (see below).

Our taxonomy follows Maitland (2000), which in turn follows Kottelat (1997), with a few exceptions such as salmonids, where Maitland (2000) is much more conservative regarding species status. This taxonomy is still in a considerable state of flux (Kottelat 1998).

Assessment of threatened status

We used Maitland (2000) as the main source of information on threat status and compared summary statistics of percentages of species under various levels of threat with the IUCN's 2003 Red List (IUCN 2003). Both sources of information used the IUCN's 1994 criteria for assessing status (IUCN 1994). However, Maitland's (2000) treatment is more comprehensive and up to date because the threat status of species appearing on the 2003 Red List had actually first been reported in 1996. In general, there was strong congruence between the two assessments, and based on further consideration of species where the assessments disagreed, we felt that Maitland's (2000) designations were better supported. For the sake of consistency, we have resisted the temptation to make ad hoc updates to the statuses of some species, pending a new assessment vetted by the IUCN. For example, we understand that *Coregonus oxyrhinchus* may

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now be extinct, *Alosa macedonica* may be endangered, and most sturgeon species are probably critically endangered. Such changes in the status of these species do not change the significance of our results.

Life history and ecological data

Life history and ecological data were derived from a variety of sources starting with Lelek (1980), Wheeler (1983), Pivnicka et al. (1992), Cihar (1998), Kirchhofer and Hefti (1996), Miller and Loates (1997), and Maitland (2000). We also made use of volumes in the Freshwater Fishes of Europe series (Holcik 1986; Hoelstlandt 1991; Banarescu and Paepke 2002; Banarescu and Bogutskaya 2003). This information was cross-checked and supplemented with journal publications and FishBase (Froese and Pauly 2003). We were able to collect data on the following variables on life histories, which were not distinguished between the sexes owing to lack of information for most of the species. Maximum size was the maximum total length (centimetres) recorded based primarily on Maitland (2000) and FishBase (Froese and Pauly 2003). Size at maturity was the minimum total length at maturity (centimetres). Age at maturity was the lower end of any range given for mature individuals in years. Maximum clutch size was the largest number of eggs recorded. This was the most widely available measure, but it was crude and ultimately unsatisfying (see Discussion). The mean trophic level was taken from FishBase (Froese and Pauly 2003), with each level denoting the number of energy transfer steps to its position in the food chain. The midlatitudinal range and total extent of latitudinal range of each species' distribution were taken from FishBase where available or else calculated from range maps or descriptions of ranges in the references cited above.

We analysed a number of habitat characteristics as follows: typical spawning substrate size (1, sand; 2, gravel; 3, stones), inclusion of vegetation as a spawning substrate (yes or no), water flow of typical habitat (1, stagnant and (or) slow; 2, wide range; 3, fast), and habitat size (1, marsh; 2, ponds and creeks; 3, springs and streams; 4, rivers; 5, lakes). We also counted the number of habitats typically occupied based on the habitats listed in "habitat size", and we assessed whether there was a general tendency toward living in running water. Although it was not always possible to score these variables precisely, our system enabled us to meet our objective, which was to ask whether threatened species were equal to, less than, or greater than closely related less threatened species in their ranks for each variable within each taxonomic paired comparison (see below).

Analyses

Most of the analyses were based on "matched pairs comparisons" between closely related species (Harvey and Pagel 1991). This involved making comparisons between related sister taxa in which one member of the pair is more threatened than the other. In nearly all cases, this entailed a comparison of taxa that were classified as least concern (i.e., nonthreatened) with taxa that were listed as threatened (e.g., vulnerable, endangered, or critically endangered). In addition to the advantage of providing statistically independent comparisons, this method also helps reduce "apples and oranges comparisons" whereby species would be pooled together that differ greatly in many biological and ecological characteristics that can create a great deal of "noise" when making comparisons (Harvey and Pagel 1991; Reynolds et al. 2001*a*). This was borne out by initial cross-species analyses, indicating that while all of the trends reported here were apparent, they were in most cases less significant.

Most of the pairings were based on taxonomy rather than strict phylogenies owing to lack of phylogenetic information, with all but one pairing occurring between species within genera (Table 1). We obtained 33 independent taxon pairs for the analyses, with a mean of 2.0 ± 1.8 SD species in the threatened side of each comparison and 2.3 ± 1.7 SD species contributing to each less-threatened category. Mean values of traits for species on each side of the comparison were used for the analyses. Although some within-genus phylogenies were available, we were unable to use them owing to lack of adequate biological information. An exception involved Acipenseridae, where phylogenetic analyses (Birstein and DeSalle 1998; Birstein et al. 2002) allowed us to use *Acipenser ruthenus* as a sister taxon to the species *Huso huso*, while other members of the genus *Acipenser* were compared with each other.

We log-transformed all continuous variables for the analyses and accepted statistical significance at $p < 0.05$.

Results

Overview of status

The European freshwater fish fauna consists of a (very) provisional total of 316 species, of which 287 are considered native, including anadromous species. These figures are subject to the caveats discussed in the Materials and methods section concerning taxonomic uncertainties, use of a conservative species concept, and an attempt to limit the scope to include species that typically spend a significant part of their life cycle in fresh water. The status of all but seven of the native species has been determined (Fig. 1). Of the native species, 47% are considered threatened (Maitland 2000). These include 88 species considered vulnerable, 38 endangered, and five critically endangered. The assessment by the IUCN (2003) is limited to 191 native species (excluding two nonnative species on their list). Of these, 29% were considered threatened and 34% were considered data deficient. The Red List considers one species to be extinct, the Turskyi dace (*Leuciscus turskyi*), which Maitland (2000) considered data deficient. The skadar nase (*Chondrostoma scodrense*) is the only species listed as extinct in the wild by Maitland (2000). The Red List categorizes it as critically endangered.

Life histories

There was no significant difference in body size between threatened and less-threatened native species, with a trend toward threatened taxa being slightly larger (paired $t_{31} = 1.233$, $p = 0.227$) (Fig. 2). However, when six pairs of anadromous species were excluded, the trend was reversed and threatened species proved to be 26% smaller than less-threatened ones (paired $t_{25} = 2.747$, $p = 0.001$) (Fig. 2). The anadromous pairs removed for this analysis were in the following genera: *Lethenteron*, *Acipenser*, *Huso*, *Alosa*, *Clupeonella*, and *Salmo*. While not all members of these genera are anadromous, removal of the individual anadromous spe-

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Table 1. Pairings of species used for the analyses.

Pair	Threatened species	Status	Less-threatened species	Status
1	*Eudontomyzon hellenicus*	CR	*Eudontomyzon danfordi*	VU
			Eudontomyzon mariae	VU
			Eudontomyzon vladykovi	VU
2	*Lethenteron zanandreai*	CR	*Lethenteron camtschaticum*	VU
3	*Acipenser baeri*	EN	*Acipenser nudiventris*	VU
	Acipenser gueldenstaedtii	EN		
	Acipenser naccarii	EN		
	Acipenser stellatus	EN		
	Acipenser sturio	EN		
4	*Huso huso*	EN	*Acipenser ruthenus*	VU
5	*Alosa alosa*	EN	*Alosa macedonica*	LR
	Alosa fallax	EN		
6	*Clupeonella abrau*	VU	*Clupeonella cultriventris*	LR
7	*Alburnus albidus*	EN	*Alburnus alburnus*	LR
			Alburnus charusini	LR
8	*Barbus cyclolepis*	VU	*Barbus barbus*	LR
	Barbus prespensis	VU	*Barbus meridionalis*	LR
			Barbus plebejus	LR
9	*Barbus macedonicus*	VU	*Barbus peloponnesius*	LR
10	*Chalcalburnus chalcoides*	VU	*Chalcalburnus belvica*	LR
11	*Chondrostoma genei*	VU	*Chondrostoma nasus*	LR
	Chondrostoma knerii	EN	*Chondrostoma oxyrhynchum*	LR
	Chondrostoma phoxinus	VU	*Chondrostoma polylepis*	LR
	Chondrostoma toxostoma	VU	*Chondrostoma prespense*	LR
			Chondrostoma soetta	LR
			Chondrostoma willkommii	LR
12	*Gobio albipinnatus*	VU	*Gobio benacensis*	LR
	Gobio banarescui	VU	*Gobio cisticaucasicus*	LR
	Gobio uranoscopus	EN	*Gobio gobio*	LR
			Gobio kessleri	LR
13	*Leuciscus aphipsi*	VU	*Leuciscus borysthenicus*	LR
	Leuciscus carolitertii	VU	*Leuciscus cephalus*	LR
	Leuciscus danilewskii	VU	*Leuciscus idus*	LR
	Leuciscus illyricus	VU	*Leuciscus keadicus*	LR
	Leuciscus microlepis	VU	*Leuciscus leuciscus*	LR
	Leuciscus polylepis	EN	*Leuciscus pyrenaicus*	LR
	Leuciscus souffia	VU		
	Leuciscus svallize	VU		
	Leuciscus ukliva	EN		
	Leuciscus turskyi	EX?*		
14	*Phoxinellus pstrossi*	EN	*Phoxinellus alepidotus*	VU
			Phoxinellus croaticus	VU
			Phoxinellus epiroticus	VU
			Phoxinellus ghetaldii	VU
15	*Pseudophoxinus beoticus*	VU	*Pseudophoxinus stymphalicus*	LR
16	*Rutilus lemmingii*	VU	*Rutilus alburnoides*	LR
	Rutilus macedonicus	VU	*Rutilus frisii*	LR
	Rutilus macrolepidotus	EN	*Rutilus rubilio*	LR
	Rutilus meidingeri	EN	*Rutilus rutilus*	LR
	Rutilus pigus	EN		
17	*Scardinius racovitzai*	VU	*Scardinius graecus*	LR
			Scardinius erythrophthalmus	LR
18	*Tropidophoxinellus spartiaticus*	VU	*Tropidophoxinellus hellenicus*	LR
19	*Vimba melanops*	VU	*Vimba vimba*	LR
20	*Cobitis calderoni*	VU	*Cobitis bilineata*	LR
	Cobitis elongata	VU	*Cobitis caspia*	LR
	Cobitis meridionalis	VU	*Cobitis caucasica*	LR

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Table 1 (*concluded*).

Pair	Threatened species	Status	Less-threatened species	Status
	Cobitis paludica	VU	*Cobitis conspersa*	LR
			Cobitis maroccana	LR
			Cobitis taenia	LR
21	*Sabanejewia larvata*	VU	*Sabanejewia balcanica*	LR
	Sabanejewia romanica	VU		
22	*Barbatula amgorae*	VU	*Barbatula barbatula*	LR
			Barbatula bureschi	LR
			Barbatula merga	LR
23	*Coregonus autumnalis*	EN	*Coregonus albula*	LR
	Coregonus oxyrhinchus	EN	*Coregonus lavaretus*	LR
			Coregonus nasus	LR
			Coregonus peled	LR
			Coregonus pidschian	LR
24	*Salmo marmoratus*	EN	*Salmo trutta*	LR
	Salmo salar	VU		
25	*Aphanius iberus*	VU	*Aphanius fasciatus*	LR
26	*Pungitius hellenicus*	EN	*Pungitius platygaster*	LR
			Pungitius pungitius	LR
27	*Gymnocephalus baloni*	VU	*Gymnocephalus acerina*	LR
	Gymnocephalus schraetser	EN	*Gymnocephalus cernuus*	LR
28	*Sander marina*	VU	*Sander lucioperca*	LR
	Sander volgensis	VU		
29	*Zingel asper*	EN	*Zingel zingel*	VU
	Zingel streber	EN		
30	*Economidichthys pygmaeus*	VU	*Economidichthys trichonis*	LR
31	*Knipowitschia goerneri*	EN	*Knipowitschia panizzae*	VU
			Knipowitschia punctatissima	VU
32	*Neogobius fluviatilis*	VU	*Neogobius cephalarges*	LR
			Neogobius gymnotrachelus	LR
			Neogobius kessleri	LR
			Neogobius melanostomus	LR
			Neogobius syrman	LR
33	*Padogobius nigricans*	VU	*Padogobius martensii*	LR

Note: Each pair consists of one or more threatened species matched with closely related species that are less threatened. LR, lower risk; VU, vulnerable; EN, endangered; CR, critically endangered; EX, extinct.

*Considered data deficient by Maitland (2000).

Fig. 1. Threat status of the 280 native species of European freshwater fishes that have been assessed by Maitland (2000) and IUCN (2003).

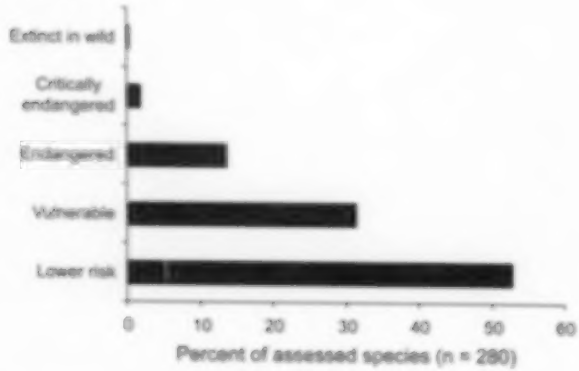
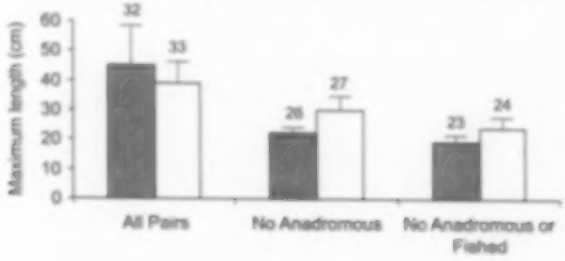


Fig. 2. Body sizes of native European freshwater fishes comparing threatened species (shaded bars) with closely related species that are less threatened (open bars). Means + 1 SE are depicted. Numbers above bars are the number of genera containing species in each category. "No anadromous" excludes pairs from six anadromous genera, and "no anadromous or fished" excludes three additional genera that include nearly all of the heavily fished species.



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cies within these genera resulted in a loss of the paired comparisons owing to lack of data for species in either the threatened or less-threatened category. The 13 anadromous species in the data set were much larger than nonanadromous ones (cross-species analysis: anadromous mean = 166.2 cm ± 33.7 SE, n = 13; nonanadromous mean = 29.2 cm ± 2.1 SE, n = 121; t_{132} = 7.572, $p < 0.001$).

It was difficult to distinguish between the effects of fishing and anadromy because most anadromous species are (or were) fished heavily, and they have all suffered from damming of waterways. Most of the other species that are fished heavily are in three genera, *Coregonus*, *Vimba*, and *Sander*, although fishing has not been implicated as the main problem faced by these species (Lelek 1980). Removal of these genera did not affect the results, with threatened species still being smaller than less-threatened ones (paired t_{22} = 2.230, p = 0.036) (Fig. 2).

Minimum size at maturity did not differ between threatened and less-threatened species, regardless of whether anadromous species were included (including anadromous, paired t_{29} = 0.281, p = 0.781; excluding anadromous, paired t_{23} = 1.276, p = 0.215) (Fig. 3*a*). Age at maturity showed similar trends and a tendency toward later age at maturity in threatened species when anadromous species were included (paired t_{12} = 1.843, p = 0.092) (Fig. 3*b*). When anadromous species were excluded, the sample size was reduced to seven pairs for which data were available, and there was no difference between threatened and less-threatened species in age at maturity (paired t_6 = 0.778, p = 0.466) (Fig. 3*b*). Removal of heavily fished species reduced the sample size to five pairs and the findings were similar (not shown).

We found no significant relationship between threat status and maximum fecundity, with a mean value of 802 975 ± 636 795 SE eggs for threatened species and a mean of 191 096 ± 79 640 SE for less-threatened species (paired t_8 = 0.124, p = 0.904). Note the enormous variation in fecundity within each threat category and the small number of pairs for which data were available.

Fig. 3. (*a*) Minimum size at maturity and (*b*) age at maturity of threatened species (shaded bars) in comparison with their nearest relatives that were less threatened (open bars) (mean + 1 SE).

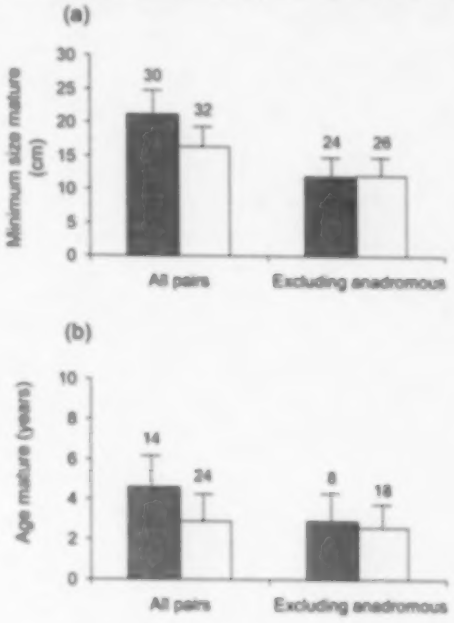
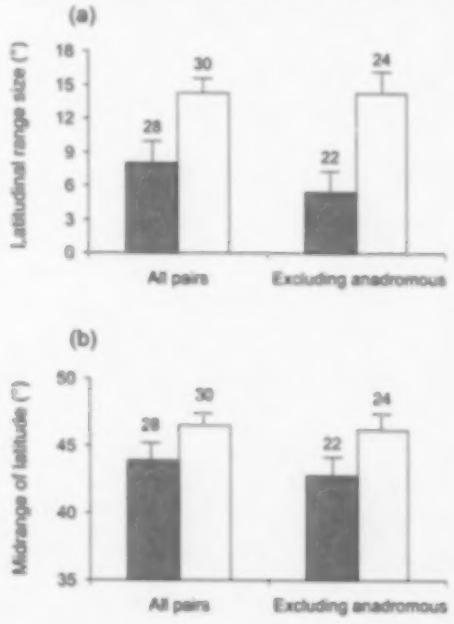


Fig. 4. (*a*) Latitudinal range size and (*b*) midrange of latitude of threatened species (shaded bars) in comparison with their nearest relatives that were less threatened (open bars) (mean + 1 SE).



Biogeography and ecology

The mean trophic level did not differ between threatened and less-threatened species (mean threatened = 3.27 ± 0.48, mean less threatened = 3.27 ± 0.46; paired t_{24} = 0.242, p = 0.811). This result was unaffected by exclusion of anadromous species (not shown).

Threatened species have latitudinal ranges that are only 56% as large as those of related taxa that are less threatened (all species, paired t_{27} = 3.003, p = 0.006) (Fig. 4*a*). Exclusion of the anadromous pairs accentuated this difference (paired t_{21} = 4.748, $p < 0.001$) (Fig. 4*a*). Threatened species also occur farther south than their less-threatened relatives (all species, paired t_{27} = 2.292, p = 0.030; excluding anadromous species, paired t_{21} = 3.186, p = 0.004) (Fig. 4*b*). These results for latitudinal range size and location remain unchanged when the three heavily fished genera are excluded (not shown).

The links described above between threat status, small body size, small range size, and southerly distribution were also tested more generally by examining correlations among these traits using cross-species comparisons. As expected from the matched pairs results, there was a strong positive correlation among all species between their latitudinal position and the extent of their latitudinal range (r = 0.54, $p <$

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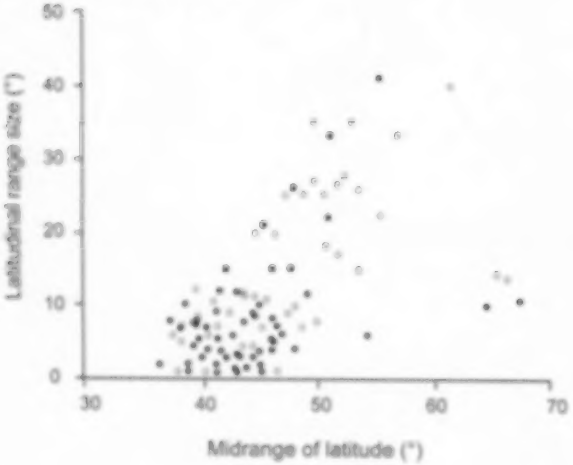
Table 2. Habitat characteristics of threatened and less-threatened species of native European freshwater fishes including anadromous species.

Variable	Threatened = less-threatened	Threatened < less-threatened	Threatened > less-threatened
Substrate size	14	3	1
Vegetation for spawning	21	3	2
Water flow	18	6	7
Habitat size	14	9	5
Number of habitats used	15	11	5
Riverine	19	4	8

Note: Data are the number of pairs in which the value for the threatened taxa is either equal to, less than, or greater than that for their less-threatened relatives for each habitat characteristic. The variables are as follows: Typical spawning substrate size: 1, sand; 2, gravel; 3, stones; inclusion of vegetation as a spawning substrate: yes or no; water flow of typical habitat: 1, stagnant and (or) slow; 2, wide range; 3, fast; habitat size: 1, marsh; 2, ponds and creeks; 3, springs and streams; 4, rivers; 5, lakes. Number of habitats used is based on the habitats listed in habitat size. Riverine denotes tendency to occupy running water.

Fig. 5. Size of latitudinal distribution versus location of the middle of each species' range. Solid circles, threatened species; open circles, species at lower risk.



0.001, $n = 94$) (Fig. 5). Visual inspection of the individual species in Fig. 5 also supports the matched pairs statistics for smaller range sizes of threatened species as well as their predominance at southerly latitudes (Fig. 4). Furthermore, with threat statuses combined, larger-bodied species had larger ranges ($r = 0.48$, $p < 0.001$, $n = 92$), which were farther north ($r = 0.34$, $p < 0.001$, $n = 96$). These correlations remained significant if anadromous and (or) the three additional heavily fished genera were excluded (not shown). The relationship between body size and midrange of latitude did not differ significantly between threatened and nonthreatened species (analysis of covariance, $F_{[1,47]} = 2.028$, $p = 0.161$). A logistic regression was used to attempt to predict whether nonanadromous species are threatened based on their body size and the midrange of their latitude. The overall predictive power was 66% correct, with 68% of nonthreatened species classified correctly and 65% of threatened species classified correctly. The relationship between threatened status and midrange of latitude is significant (logistic regression $p = 0.034$), whereas the relationship with body size is weaker ($p = 0.103$).

The search for habitat differences among threatened species and less-threatened close relatives did not reveal strong patterns in the paired comparisons (Table 2). There were nonsignificant trends for threatened species to live in smaller habitats (9/14 taxon pairs in which we could discern differences in habitat size) and threatened species tended to live in fewer habitats (11/16 pairs in which habitat number differed) (g tests, $p > 0.05$). They also tended to be more "riverine" (9/14 pairs). Exclusion of six anadromous genera and (or) three additional heavily fished genera did not alter these results (not shown). These results were largely unchanged in cross-species analyses, which ignore phylogenetic pairings, with the tendency for threatened species to occupy fewer habitats becoming significant (threatened mean = 1.6 ± 0.7 SD, nonthreatened mean = 1.9 ± 0.8; $t_{117} = 2.110$, $p = 0.037$).

Discussion

The phylogenetically based comparisons in this study reveal that for European fish species whose life cycles are entirely restricted to fresh waters, threatened species are smaller bodied than species that are at lower risk. Inclusion of anadromous species reverses this trend. We found no differences in minimum size at maturity or in age at maturity. Threatened species have narrower latitudinal distributions, which are more southerly than those of lower-risk species. Threatened species do not have different trophic positions, and there were nonsignificant tendencies toward occupation of fewer habitats, which are more riverine. Most of these findings are contrary to the patterns that have been found in studies of marine fishes. Furthermore, they contradict some previous studies of freshwater fishes. Below, we try to resolve these discrepancies in light of theories concerning links between life histories, population ecology, and conservation.

The traditional prediction has been that species of animals with fast life histories, i.e., short generation times and associated traits such as small body size, should be able to persist better and recover more quickly from threats caused by humans (reviewed by Reynolds 2003). This prediction has been confirmed by studies of marine fishes that are exploited commercially (Jennings et al. 1998; Denney et al. 2002; Hutchings and Reynolds 2004). Furthermore, when species are exploited directly by humans, large-bodied species are

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usually preferred and more susceptible to capture. These generalizations are true not only for commercially exploited fishes but for most other exploited taxa as well, including mammals (Peres 2000; Purvis et al. 2000) and birds (Owens and Bennett 2000). However, this result depends critically on direct mortality being the main threat (Reynolds 2003). If habitats are destroyed, life histories may be much less relevant to susceptibility of populations. For most freshwater fishes, habitat degradation has been the primary cause of extinction, through physical alterations such as damming, canalization, and water abstraction and pollution, with additional problems from the introduction of alien species and overfishing (Harrison and Stiassny 1999). These problems may affect small-bodied species as much as they impact upon large-bodied ones. Indeed, it has been suggested that in many regions, the impacts on freshwater habitats may be so severe that life histories may simply be irrelevant (Duncan and Lockwood 2001).

Our finding that relationships between body size and threat status depend on whether or not anadromous species are included in the analyses supports the arguments above concerning the importance of distinguishing among threats. Most anadromous species suffer acutely from physical blockage of waterways, are large bodied, and are (or were) fished heavily (e.g., Elvira 1996; Keith and Allardi 1996). When we exclude anadromous species, as well as additional species that are fished heavily, we are left with species in which fishing plays little if any role in their threat status (Lelek 1980). This breaks the predicted link between large body size and susceptibility. Indeed, we find that smaller-bodied species are under greater threat than their larger-bodied relatives.

Why should smaller-bodied species face a greater risk of extinction than larger-bodied ones? We did not find compelling links between threat status and habitat specialization, although there was a trend for threatened species to occupy fewer habitats. Arguably, there may be an element of circularity in the latter trend, since some species are confined to single watersheds or water bodies. At this extreme, threat status based on range size will be correlated with "narrowness" of habitat usage. More important is the fact that many small-range endemics will have been listed as threatened on the basis of their range size, which accounts for many of the narrow latitudes illustrated here. This result by itself cannot explain the body size patterns. We believe the main reason for small-bodied species being under greater threat lies in our finding that they tend to occur farther south. Regions such as the Iberian Peninsula and Greece support many small-range endemics that are naturally "rare" in terms of range size but also suffer additional threats from humans. For example, 12 of the 19 Iberian endemics are considered endangered, with the key problems being habitat destruction, pollution, and exotic predators (Economidis 1995; Elvira 1996; Bernardo et al. 2003). Overfishing has not been implicated in the endangerment of any of these species, whereas the combination of overfishing and the presence of about 11 000 large dams has led to all anadromous species being classified as threatened.

This study was limited by availability of fundamental life history and ecological data for many species, although the situation is far better in Europe than in most other parts of the world (Lundberg et al. 2000). The fecundity data were sparse and highly imprecise and ultimately probably meaningless for the comparisons. Similarly, it is difficult at present to produce objective descriptions of ecological requirements of most species, so the nonsignificant trends reported here should also be regarded as preliminary. As noted in the Materials and methods section, our knowledge of threat status of many species is improving rapidly, with the potential for a full revision in the future. We tried various permutations of the analyses to account for a number of upgrades and downgrades of the status as currently published and found that our overall findings were robust. Finally, Kottelat (1997) has pointed out that we still have much to learn about the systematics and nomenclature of European fish species. As we learn more about species boundaries and relationships, it will become possible to go beyond the conservative use of matched pairs comparisons within genera that we have explored here, taking advantage of the full range of phylogenetic relationships among taxa.

In conclusion, this study has found that threatened species of European freshwater fishes are smaller bodied, have smaller latitudinal range sizes, and occur farther south than close relatives that are less threatened. The body size relationship disappears when anadromous species are included, suggesting that links between life history traits and risk of extinction depend on relationships between migratory behaviour and threats such as blockage of waterways and fishing. Future progress in studies of the biology of vulnerability in fishes and other taxa may come from further analyses that distinguish explicitly between various threatening processes, overlaid onto finer-scale mapping of specific threats onto distributions.

Acknowledgements

We thank Brian Shuter, Peter Abrams, and Erin Dunlop for inviting us to a stimulating symposium on life histories and fisheries at the American Fisheries Symposium in Québec in August 2003. Jörg Freyhof warned us about a number of anomalies in the statuses of fishes as currently published, leading to various permutations of the analyses to verify the overall robustness of our results.

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The role of dispersal and demography in determining the efficacy of marine reserves[1]

Leah R. Gerber, Selina S. Heppell, Ford Ballantyne, and Enric Sala

Abstract: Marine reserves are rapidly becoming an important tool for protection and recovery of depleted marine populations. However, the relative value of reserves to particular species is strongly dependent on its life history and behavior. We present a general conceptual framework for considering dispersal in simple demographic models. This framework includes transition matrices that consist of two age-structured models connected by transition probabilities for general migration, ontogenetic shifts, and recruitment in both a reserve and an unprotected area. We show that life history characteristics and perturbation analysis can be used to predict changes in growth rate due to a decrease in adult mortality resulting from a marine reserve for different levels and types of dispersal. Reserves enhanced growth rate for all species irrespective of net dispersal between the reserve and surrounding matrix habitat, but the efficacy of reserves relative to catch reduction depended significantly on the magnitude and sign of net dispersal across the reserve boundary. Patterns of reserve efficacy across different dispersal types were strongly species specific. Given the paucity of spatially explicit data for many marine systems and species, this simple approach represents a first step in applying life history information to advance current theory and provide practical considerations for marine reserve management.

Résumé : Les réserves marines sont vite en train de devenir des outils importants pour la protection et la récupération des populations marines décimées. Cependant, la valeur relative des réserves pour une espèce en particulier dépend de son cycle biologique et de son comportement. Nous présentons un cadre conceptuel général pour examiner la dispersion dans des modèles démographiques simples. Ce cadre comprend des matrices de transition qui consistent en deux modèles structurés d'après l'âge reliés par des probabilités de transition pour la migration générale, les changements ontogéniques et le recrutement dans une zone de réserve et dans une zone sans protection. Nous montrons que les caractéristiques démographiques et l'analyse de perturbation peuvent servir à prédire les changements du taux de croissance causés par un déclin de la mortalité des adultes associé à la présence d'une réserve marine pour divers degrés et types de dispersion. Les réserves font augmenter le taux de croissance chez toutes les espèces, quelle que soit la dispersion nette entre la réserve et la matrice d'habitats avoisinants; cependant, l'efficacité de la réserve, par comparaison à une réduction des captures, dépend de façon significative de l'importance et du signe de la dispersion nette à travers les frontières de la réserve. Les patrons d'efficacité des réserves en fonction des types de dispersion varient fortement selon les espèces. Étant donné le peu de données spatiales spécifiques sur de nombreux systèmes marins et espèces de mer, cette approche simple représente un premier pas vers l'application des données démographiques pour améliorer la théorie actuelle et pour fournir des informations pratiques pour la gestion des réserves marines.

[Traduit par la Rédaction]

Introduction

The benefits of no-take marine reserves are many, including an increase in size and biomass of target species and local enhancement of fisheries (Allison et al. 1998; National Research Council 2001; Gell and Roberts 2003). The role of dispersal in marine protected area design has been addressed by a number of researchers, both empirically (e.g., Martell et al. 2000; Grantham et al. 2003) and theoretically (Quinn et al. 1993; Stockhausen et al. 2000; Botsford et al. 2001), although rarely in a comparative framework (but see Polacheck 1990; Acosta 2002; Lockwood et al. 2002). Dispersal may be modeled simply as diffusion into and out of a reserve, spillover in response to density dependence, or directed dispersal due to migration or ontogenetic shifts in habitat use that are life history dependent. The latter, in particular, has been overlooked in most theoretical treatments of marine reserves, in spite of the fact that most marine spe-

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L.R. Gerber.[2] School of Life Sciences, Arizona State University, College and University Drive, Tempe, AZ 85287-1501, USA.
S.S. Heppell. Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, OR 97331, USA.
F. Ballantyne and E. Sala. Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, CA 92093-0202, USA.

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[2]Corresponding author (e-mail: leah.gerber@asu.edu).

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cies undergo major habitat shifts at least once in their life history.

Because marine species typically exhibit complex life histories with multiple ontogenetic shifts (e.g., directed spillover between habitats that occurs when individuals move from one life stage to the next), only under rare circumstances would a reserve encompass the entire life cycle of a species or population. Likewise, patchy distribution of resources forces many marine species to disperse long distances, even within a life stage, and migration across reserve boundaries that are fixed in space and (or) time is certain to impact population dynamics. Theoretical studies suggest that reserves should provide fewer benefits to species with greater rates of dispersal as adults (see review by Gerber et al. 2003). Therefore, species with moderate rates of dispersal are good candidates for reserves because high adult dispersal allows for too little protection of reproductive output within reserves, and low adult dispersal does not increase catch outside reserves. But, from a purely conservation standpoint, evidence suggests that marine reserves appear to be most effective for both preventing extinction and promoting recovery for those species that exhibit a low population growth rate (λ) and a low dispersal rate (Gerber et al. 2002).

Any approach to comparing the efficacy of reserves has to be developed in the context of the objective of the reserve (Agardy 1994). Possible objectives for enhancement of particular species could be to maximize population abundance and yield, to minimize rate of population decline, or to minimize the probability that the population falls below some quasi-extinction threshold. The potential effects of reserves on single species can only be determined with the incorporation of spatial and demographic information. The previously popular assumption of a common pool of larval dispersal is inadequate (Gaines et al. 2003) owing to species-specific differences in the spatiotemporal distribution of larvae; hence, metapopulation structure and connectivity (via migration or larval dispersal) need to be incorporated into reserve design and evaluation. In addition, demography needs to be taken into account because reserve effects vary as a function of life histories (Hooker and Gerber 2004).

In this paper, we propose that modeling tools based on life history theory can be used by decision makers to design marine reserves for target species and by managers to evaluate the efficacy of different reserve designs. Our measure of efficacy is the change in the maximum eigenvalue of a deterministic projection matrix with a proportional change in mortality. Our assumption is that maximizing the λ of a population should have a significant impact on population recovery and spillover, an important objective for fishery enhancement. We present a conceptual framework using simple spatial matrix population models that incorporate life history and dispersal information (Wooton and Bell 1992; Doak 1995) to determine the efficacy of marine reserves as a function of spatial and demographic parameters.

Methods

A conceptual framework for evaluating the importance of life history and dispersal in reserve efficacy

Four conceptual models for the role of dispersal in simple life history models are illustrated (Fig. 1). The selection of the appropriate model will depend on the particular life history and dispersal mechanism of the focal organism. Our general conceptual model includes transition probabilities for general migration (spillover), ontogenetic shifts, and recruitment (e.g., larval dispersal) between a reserve and an unprotected area. We illustrate a situation in which the primary mechanism of dispersal between the protected area and unprotected area is recruitment (Fig. 1*a*). Here, animals spend their whole lives in one location or the other, with low mobility. This scenario might be appropriate for sessile invertebrates (e.g., urchins), where larval dispersal between sites outweighs adult and juvenile dispersal. We then describe a situation in which adults and (or) juveniles move between protected and unprotected sites, with insignificant larval or newborn exchange (Fig. 1*b*). Migration into and out of the reserve may occur as spillover in the adult, juvenile, or both adult and juvenile stages. Also depicted is a situation in which exchange between sites only occurs as individuals undergo an ontogenetic niche shift between protected and unprotected sites (Fig. 1*c*). Ontogenetic shifts in habitat use occur for many reef fish species, which move from estuarine to pelagic environments between the juvenile and adult life stages. Here, a reserve established for a particular habitat will have stronger impacts on the life stage that occupies that habitat. A variation of this scenario is one in which the reserve protects only the breeding or nesting grounds of species, such as the spawning sites of groupers (e.g., Sala et al. 2003) or turtle nesting beaches. In these cases, individuals tend to make their way into the reserve after a particular life stage and only for short periods of time. When spawning, calving, or pupping areas are protected, the net effect is that those adults are in the reserve for that year or portion of a year, with higher survival or offspring production rates, even if they are not physically in the reserve all the time. The generic model (Fig. 1*d*) allows explicit incorporation of any or all of these transition probabilities. Below, we illustrate the application of this framework for four representative life histories of species in the Gulf of California and Baja California to examine the role of dispersal at different life stages in reserve efficacy.

Developing a spatial demographic model for evaluating reserve efficacy

We used our conceptual framework to examine two questions: (*i*) does dispersal reduce the efficacy of reserves for species that are otherwise predicted to respond strongly assuming no dispersal, and (*ii*) how does dispersal increase the efficacy of reserves for species that are otherwise predicted to show very little response from their establishment because of slow demographic rates? For a representative range of life histories for marine species, we examined the degree to which dispersal between a reserve area and a nonreserve area mitigates the effect of a reduction in adult mortality on reserve efficacy using the approach of Gerber and Heppell (2004). The species we chose as case studies (goliath grouper (*Epinephalus itajara*), sea urchin (*Tripneustes ventricosus*), loggerhead sea turtle (*Caretta caretta*), and gray whale (*Eschrichtius robustus*)) (Table 1) exhibit different types of dispersal and a wide range of mortality, which could be reduced by protected areas.

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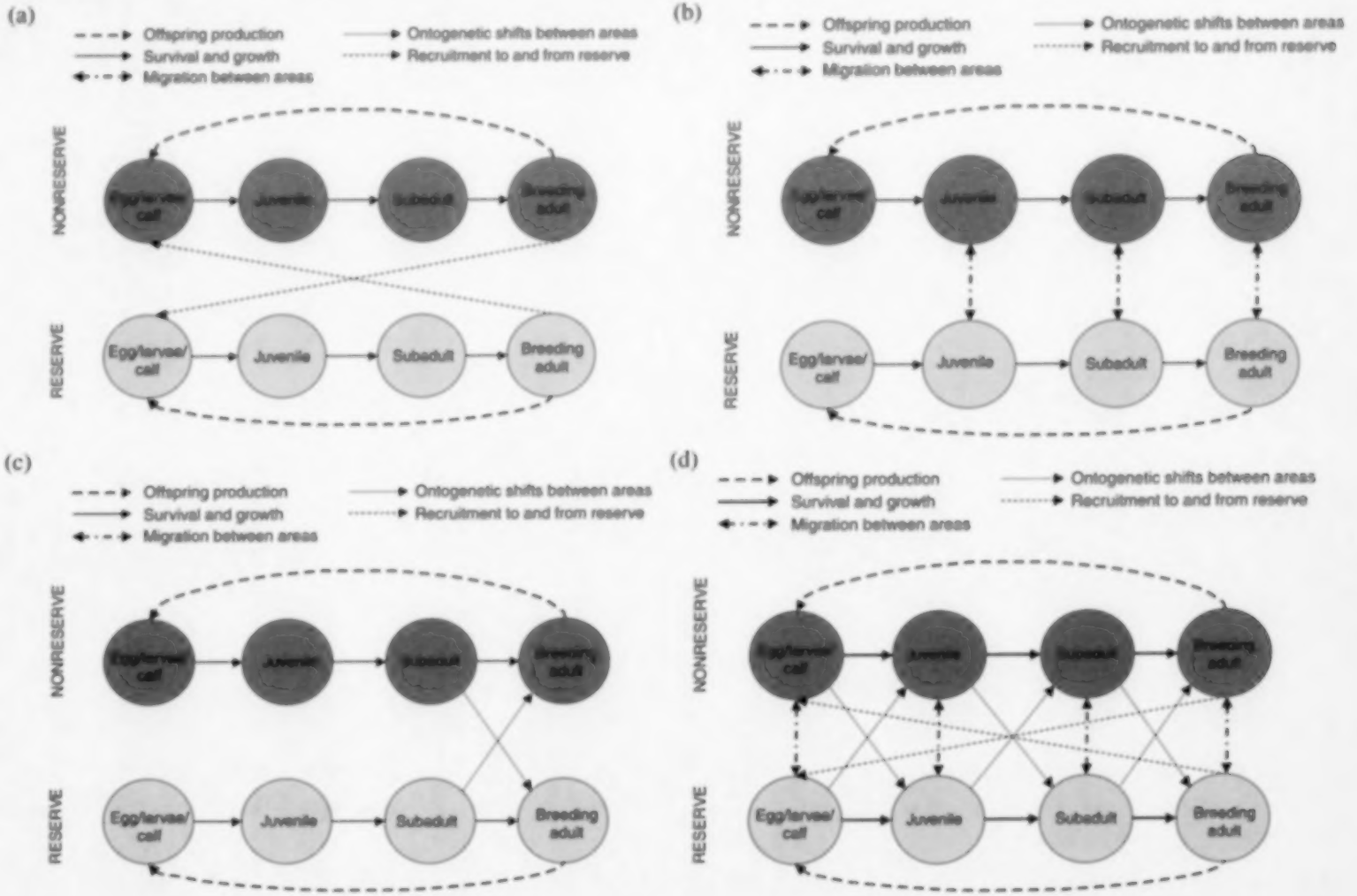
Fig. 1. Conceptual framework for considering dispersal in simple demographic models. The model includes transition probabilities for general migration (spillover), ontogenetic shifts (directed spillover that occurs when individuals move from one life stage to the next), and recruitment (e.g., larval dispersal) in both a reserve and an unprotected area. (*a*) A situation in which the primary mechanism of exchange is recruitment of larvae or newborns; (*b*) a situation with random exchange (spillover) among adults and (or) juvenile life stages but insignificant larval or newborn exchange; (*c*) similar to *b*, but specifies an ontogenetic shift in habitat use between sites; (*d*) a generic model that allows explicit incorporation of any or all of these transition probabilities.



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We constructed a two-site matrix model for each species, with two patches representing a reserve and an unprotected population (Morris and Doak 2002). Each patch matrix was age structured with adults grouped into a single stage (Heppell et al. 2000). Vital rates and stages are provided (Table 1). In our model, dispersal between populations can be incorporated into the same general form of simple matrix models. The inclusion of dispersal results in the following two-patch matrix, where M represents dispersal for each matrix transition:

$$\begin{bmatrix} 0 & 0 & \cdots & P_{\alpha-1}(1-M_{AB})F_A & P_\alpha(1-M_{AB})F_A & 0 & 0 & \cdots & P_{\alpha-1}M_{BA}F_A & P_\alpha M_{BA}F_A \\ P_1(1-M_{AB}) & 0 & 0 & 0 & 0 & P_1M_{BA} & 0 & 0 & 0 & 0 \\ 0 & P_2(1-M_{AB}) & \ddots & \vdots & \vdots & 0 & P_2M_{BA} & \ddots & \vdots & \vdots \\ 0 & 0 & P_{\alpha-2}(1-M_{AB}) & 0 & 0 & 0 & 0 & P_{\alpha-2}M_{BA} & 0 & 0 \\ 0 & 0 & 0 & P_{\alpha-1}(1-M_{AB}) & P_\alpha(1-M_{AB}) & 0 & 0 & 0 & P_{\alpha-1}M_{BA} & P_\alpha M_{BA} \\ 0 & 0 & \cdots & P_{\alpha-1}M_{AB}F_B & P_\alpha M_{AB}F_B & 0 & 0 & \cdots & P_{\alpha-1}(1-M_{BA})F_B & P_\alpha(1-M_{BA})F_B \\ P_1M_{AB} & 0 & 0 & 0 & 0 & P_1(1-M_{BA}) & 0 & 0 & 0 & 0 \\ 0 & P_2M_{AB} & \ddots & \vdots & \vdots & 0 & P_2(1-M_{BA}) & \ddots & \vdots & \vdots \\ 0 & 0 & P_{\alpha-2}M_{AB} & 0 & 0 & 0 & 0 & P_{\alpha-2}(1-M_{BA}) & 0 & 0 \\ 0 & 0 & 0 & P_{\alpha-1}M_{AB} & P_\alpha M_{AB} & 0 & 0 & 0 & P_{\alpha-1}(1-M_{BA}) & P_\alpha(1-M_{BA}) \end{bmatrix}$$

This is a general model intended to illustrate the range of possible dispersal scenarios and ontogenetic shifts between different life stages to and from the protected area (see Fig. 2). The model (shown in age-structured form, where each row–column represents a single age-class for juveniles, and adults are grouped into one stage) contains two single-site matrices: A, the unprotected site, and B, the reserve site. The parameters P_i represent mean annual survival probabilities for age-class i, and F_A and F_B are the mean annual fertility rates outside and inside the reserve, respectively. The length of the juvenile stage is dependent on age at maturity, α (Table 1). The matrices in the other two quadrants reflect transitions between patches from A to B (lower left) or B to A (upper right). The postbreeding census format results in an annual sequence for each age-class of survival, migration, and reproduction. Thus, a reproduction term is applied to the last age-class of juveniles, which are animals that will mature (if they survive), migrate, and breed before the census. For example, $P_{\alpha-1}M_{AB}F_B$ represents the probability of maturing juveniles that are in the unprotected area migrating into the reserve and breeding for the first time (e.g., through an ontogenetic shift). Note that for our examples, ontogenetic shifts M_{AB} and M_{BA} only occur at age 0 or age $\alpha - 1$. Also, although movement probabilities from patch i to j are given by M_{ij}, we do not necessarily assume all of these to be the same.

For our four examples, the life stage in which dispersal occurs varies among species (Tables 1 and 2). A constant migration probability is assigned to the age 0 class (eggs or newborns), juvenile age-classes, or the adult stage for each submatrix. Because in the real world, reserves are much smaller than unprotected areas, our model allows the probability of moving in and out of the reserve probabilities to differ (i.e., M_{AB} need not be equal to M_{BA}).

The projection matrix maps a vector of population sizes in one time unit onto the vector of population sizes in the next unit. This vector represents population size in each age-class (e.g., the number of individuals in ages-classes 0, 1, 2,..., α, where α is adult) for sites A and B. The number of adults in one time unit in patch A is the sum of the number of last-stage juveniles in patch A the previous time unit that survive and do not move plus the number of adults from the previous time unit in patch A that survive and do not move plus the number of adults and subadults from the previous unit in patch B that survive and migrate out of the reserve. The time interval for all models is 1 year, so we assume that adults are either protected or not for an entire year. Adults that migrate to a reserve for breeding are not in that location year-round but do experience a lower annual mortality because they are there for part of the year. In the case of marine mammals, at least, this would also improve fecundity for those individuals that breed in the reserve.

Using this model, we evaluated how life history and a reduction in mortality interact to determine λ for the two-patch matrix created for each species (see Fujiwara and Caswell (2001), Kareiva et al. (2001), and Gerber and Heppell (2004) for an explanation of survival versus mortality sensitivity). For each case study, we made the simplifying assumption that establishing a reserve reduces adult mortality by 20% at site B, where mortality is 1 – annual survival probability. We then evaluated the effect of dispersal during different life stages on λ calculated for the entire two-patch matrix. We focus on a reduction in adult mortality because, in general, adults are the focus of a fishery, and thus, we seek to measure the potential impact of reserves based on protection of this life stage. For simplicity, we assume that all mortality is fishing mortality (e.g., $1 - P_\alpha$ is multiplied by 0.8). We compared the simplest reserve model with a generic reduction in adult mortality (e.g., as would occur with a constant mortality reduction analogous to a quota management scenario), where there is no effective reserve and mortality is reduced in sites A and B by 10%; we then included multiple forms of dispersal and timing of dispersal for two different dispersal rates.

How does dispersal rate interact with life history to determine reserve efficacy?

First, we compared population λ values for models with different dispersal rates to a constant mortality reduction (with no dispersal) in which mortality is reduced by 10% for both patches (versus the reserve system where mortality is reduced by 20% in one patch). For gray whales and sea turtles, we considered the effect of adult dispersal, and for sea urchins and groupers, we considered the effect of larval dis-

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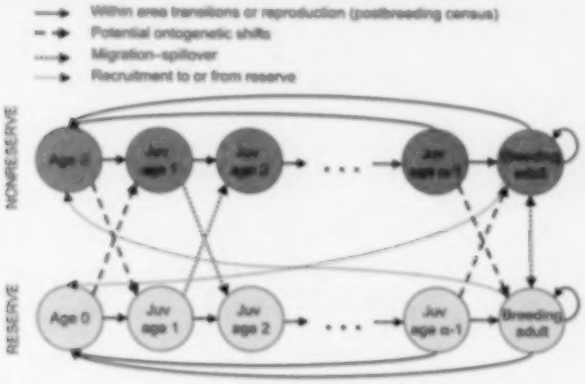
Table 1. Life history parameters assumed in demographic models.

Species	Age categories (matrix dimensions)	Fecundity (eggs·year^{-1})	Age at maturity	Age 0 survival rate	Adult and juvenile survival	Juvenile habitat	Adult habitat	Type of dispersal modeled in Fig. 3
Goliath grouper (*Epinephelus itajara*)	0–5+ (12)	75 000[a]	4–6[b]	0.000 007[c]	0.85[c]	Shallow bays and estuaries	Structure in near and offshore	Recruitment
Sea urchin (*Tripneustes ventricosus*)	0–3+ (8)	2 000 000[d]	4[e]	0.000 001[d]	0.72, 0.5[d]	Rocky subtidal	Rocky subtidal to 30 m	Recruitment
Loggerhead sea turtle (*Caretta caretta*)	0–22+ (46)	153[f]	21[g]	0.5[c]	0.809, 0.705[c]	Open ocean, nearshore	Nearshore	Adult breeding reserve
Gray whale (*Eschrichtius robustus*)	0–8+ (18)	0.47[h]	8[h]	0.893[h]	0.944, 0.893[h]	Shallow bays	Nearshore	Adult reserve

[a]Fertility estimated to solve for $\lambda = 1$; λ is population growth rate.
[b]Bullock et al. (1992).
[c]Sadovy and Eklund (1999).
[d]Pfister and Bradbury (1996).
[e]Crowder et al. (1994).
[f]Reilly (1984).

Fig. 2. General model used for perturbation analysis illustrating possible dispersal scenarios and ontogenetic shifts between different life stages to and from the protected area.



persal in reserve efficacy (Fig. 2), although we are aware that groupers can exhibit important spawning migrations (Sadovy and Eklund 1999). While limited data on dispersal distances are available for these species, we examined the sensitivity of reserve efficacy (i.e., increase in λ) to a range of dispersal scenarios to evaluate the relative importance of dispersal in predicting the effects of reserves based on life history. Parameter values for model scenarios are defined (Table 2*a*). This analysis helps to identify how changes in dispersal and vital rates affect reserve efficacy for each model. However, this simple approach does not allow for the additional dispersal patterns and ontogenetic shifts that exist in these four species (e.g., grouper exhibit juvenile ontogenetic shifts).

How does dispersal mechanism interact with life history to determine reserve efficacy?

To explore the degree to which the details of dispersal matter, we then evaluate how life history and various modes of dispersal interact to determine the efficacy of reserves. For each species, we considered the impact of including each single mechanism of dispersal as defined above on reserve efficacy. We examined the relative impact of each mechanism of dispersal for two different dispersal rates (low and high dispersal from reserve to unprotected site; Table 2*b*). In light of the paucity of dispersal data for these species, our intention here was not to parameterize realistic models for each species. Thus, while no single scenario encompasses the full range of biological complexity for the species considered, our intention is to compare the relative importance of each single dispersal mechanism to reserve efficacy.

Results

Results may be interpreted as general differences between four representative heuristic models for marine species. Models with dispersal may or may not differ from what we would predict from elasticity analysis of the life cycle (sensu Gerber and Heppell 2004). The spatial perturbation analysis approach used in this study is not specific to marine reserves as a management tool (i.e., perturbation analysis can be applied to examine a suite of hypothesized threats and po-

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Table 2. Dispersal parameters in model scenarios used to generate (*a*) Fig. 3 and (*b*) Fig. 4.

(*a*) Model scenario.	M_{AB}	M_{BA}
No dispersal into reserve	0	0
High dispersal out of reserve (small reserve)	0.1	0.9
High dispersal into reserve (large reserve)	0.9	0.1
Total mixing (reserves are of equal size or attractiveness)	0.5	0.5
(*b*) Dispersal scenario.	High or low M applied to:	
Recruitment	P_0	
Adult spillover	P_{ω}, $P_{\omega}F$	
Juvenile spillover	P_0, P_1,..., $P_{\omega-1}$	
Adult breeding reserve (ontogenetic shift)	$P_{\alpha+1}$, P_{ω}, $P_{\alpha+1}F$, $P_{\omega}F$	
All-age spillover	P_0, P_1,..., P_{ω}, $P_{\alpha+1}F$, $P_{\omega}F$	

Note: (*a*) For gray whales and turtles, dispersal is modeled as adult spillover; for urchins and groupers, dispersal is modeled as recruitment. Adult mortality is reduced by 20% in the reserve site for all dispersal scenarios and by 10% in both the reserve and nonreserve sites for the catch reduction scenario. (*b*) Dispersal parameters in model scenarios for high dispersal out of the reserve (Fig. 4*a*) and high dispersal into the reserve (Fig. 4*b*). For all scenarios, adult mortality is reduced by 20% in the reserve site.

tential management strategies that are species or location specific).

How does dispersal rate interact with life history to determine reserve efficacy?

For our first analysis, the change in λ resulting from a decrease in adult mortality and stage-specific dispersal varied for each representative life history (Fig. 3). It should be noted, however, that the effects on λ caused by vital rate values and age at maturity are confounded with model structure in the first analysis (e.g., dispersal occurs in different stages for urchins and whales). With this in mind, comparisons can be made between species and for different model scenarios for each species. Overall, sea urchins and groupers exhibited the most striking response to the establishment of a reserve, while whales and sea turtles exhibited a smaller absolute increase in λ following a decrease in adult mortality (also see Gerber and Heppell 2004). The maximum increase in λ is achieved when there is no dispersal, as the dominant eigenvalue for the metapopulation matrix is driven by the submatrix with the highest λ (site B).

The predicted change in λ for all species was reduced when dispersal was added to the model. The effect of dispersal is to proportionately reduce the maximum benefit attainable by the reduction in mortality that occurs in the reserve because individuals "leak out" and the net reduction in mortality is reduced. Thus, the magnitude and sign of net dispersal across the reserve boundary had strong effects on the efficacy of reserves for all species, but the responses took on the same shape for all four species. Under the reduced catch scenario, the change in λ was half of that expected from the no-dispersal scenario. The efficacy of reserves relative to catch reduction or the maximum benefit possible depended significantly on net dispersal (Fig. 3). When net dispersal was negative (i.e., higher dispersal out of reserve), efficacy was lower than that of catch reduction for all four species.

For these models, reserves were most effective when dispersal in both directions was zero. In this type of model, source (reserve) and sink (fished) habitats are disconnected and fisheries have no access to stocks protected within the reserve boundary; thus, the reserve effects are pronounced and the asymptotic population λ is entirely driven by dynamics inside the reserve. This is because the population size of the reserve eventually becomes arbitrarily large relative to the unprotected site so that the growth of the population as a whole approaches that of the reserve site. This dynamic may be prevented by finite patch size in real systems, where the protected area is likely to be smaller than the unprotected area. Thus, our method will be most useful for looking at responses to small changes in mortality when populations in both patches are initially rather close to equilibrium. Nonetheless, reserves have only slightly lower efficacy when dispersal is net positive (emigration < immigration) and still higher efficacy than fisheries reduction. When reserved and nonreserved populations mix equally, reserves and fisheries reduction have nearly equal efficacy for all case studies.

The consistency of reserve efficacy across taxa suggests that dispersal may indeed override life history considerations when setting reserves. More specifically, if the dispersal of a target species from a reserve is high relative to the replacement of these emigrants from external habitats, reserves may be a less effective tool than more traditional methods of fisheries management. In this case, reserves may be merely

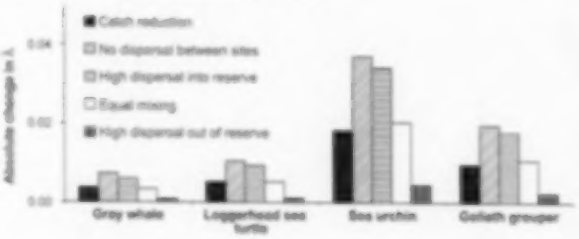

Fig. 3. Absolute change in population growth rate (λ) resulting from a 20% reduction in adult mortality due to reserves for different rates of migration modeled with four species life histories. The change in λ when there is no dispersal between the two sites is equal to the change expected from the mortality decrease alone. Mortality is reduced by 10% for both patches for the catch reduction scenario (no reserve). Parameter values for dispersal scenarios are defined in Table 2*a*.

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"show-and-tell" boundaries set over well-mixed fishing grounds.

How does dispersal mechanism interact with life history to determine reserve efficacy?

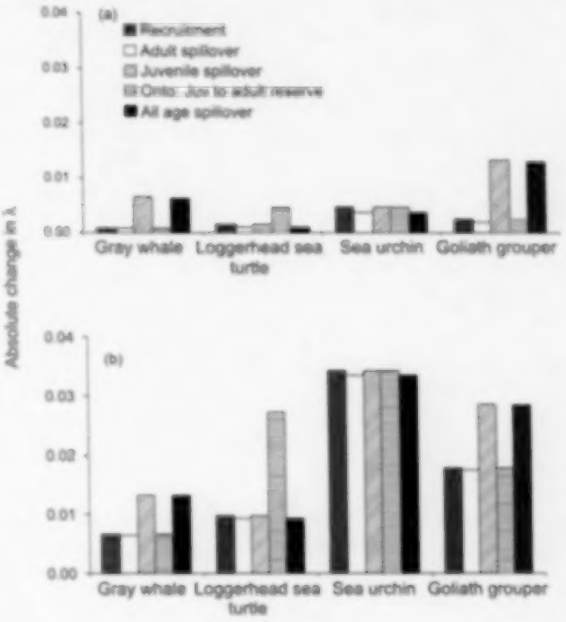
In our second analysis we examine how dispersal at different life stages (versus different net rates; Fig. 3) determines the efficacy of reserves for the same four species. Reserves increased population λ values of all species much more strongly when net dispersal into the reserve was high (compare Figs. 4*a* and 4*b*), echoing results from our first analysis. Reserves had stronger effects on groupers and whales when the model assumed juvenile or adult and juvenile spillover (Fig. 4). Thus, as long as juveniles disperse from the reserve into the fished matrix, reserves will increase population λ values of whales and groupers more than catch reduction. By contrast, reserves had the strongest effect on turtles when dispersal occurred as an ontogenetic niche shift for maturing juveniles, and urchins showed similar responses to reserves for all dispersal scenarios (Fig. 4). This is most likely due to differences in the elasticity values of adults versus juveniles (see Gerber and Heppell 2004). Finally, the relative effects of ontogenetic dispersal were similar when net dispersal was negative (Fig. 4*a*) or positive (Fig. 4*b*). In general, patterns of reserve efficacy across different dispersal types were strongly species specific.

Discussion

Studies of marine reserves have highlighted the importance of dispersal (especially larval transport; Gaines et al. 2003) and life history (Gerber and Heppell 2004) in maximizing conservation goals in the face of harvest. This paper illustrates how a more general theory of marine reserves should include both. Our results convey the importance of dispersal in determining reserve efficacy and more generally in interpreting the results of simple demographic models that ignore dispersal. In addition to the general message that dispersal matters, our results highlight the importance of understanding particular mechanisms of dispersal. Furthermore, the results convey the lack of generality among species in responses to relative importance of migration, ontogenetic shifts, and recruitment. This highlights the importance of including detailed information in both empirical and theoretical investigations of reserve efficacy.

Categorizing life histories according to their response to changes in stage-specific mortality may provide a useful method for considering conservation options (Heppell et al. 2000; Gerber and Heppell 2004). Demographic sensitivity analysis allows researchers to analyze a priori how much a small change in a demographic rate (here, adult survival) influences a population's potential for recovery. Further, such approaches rely on minimal data (e.g., survival and fecundity rates) and may allow researchers to predict the effects of alternative management actions (Heppell et al. 1999). In the context of marine reserves, these analyses must be spatially explicit to cope with the connectivity between protected and unprotected populations determined by migration, larval transport, and ontogenetic habitat shifts. We showed that life history theory can be used to predict changes in λ resulting from a decrease in adult mortality following establishment of a marine reserve for four species with different life histories and further illustrate the complexity of including different types of dispersal for species with complex life histories. Given the paucity of spatially explicit data for many marine systems, our simple approach represents a first step in applying life history information to advance current theory and provide practical considerations for marine reserve management.

Fig. 4. Absolute change in population growth rate (λ) resulting from a 20% reduction in mortality due to reserves for each dispersal mechanism for (*a*) high dispersal out of the reserve and (*b*) high dispersal into the reserve. Parameter values for the scenarios for migration, ontogenetic shifts, and recruitment are defined in Table 2*b*.



These results are consistent with current theory concluding that moderate rates of juvenile and adult dispersal render reserves more effective because high adult dispersal allows for too little protection of reproductive output within reserves, and low adult dispersal allows no increase in catch outside the reserves per unit area protected (Botsford et al. 2003; Gerber et al. 2003 and references therein). Furthermore, our results suggest that, in addition to higher population recovery rates following reserve implementation for species with high reproductive output (e.g., urchins and groupers), those with high larval dispersal may benefit more than those with high adult dispersal (e.g., whales and turtles). Our explicit consideration of recruitment from the unprotected area to the reserve has been largely ignored in theoretical and empirical studies of reserve efficacy.

Further assessment, both theoretical and empirical, is needed to develop driving principles for reserve design and life history attributes. A more systematic evaluation of the effect of variation in cofactors (e.g., stage-specific dispersal and demography) is an important next step. Explicitly incorporating uncertainty in vital rates is also critical to the application

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of demographic analysis to marine reserve design. Finally, an important next step will be to include density-dependent population growth in this type of modeling framework. While our model assumes that growing fast is more important than the ultimate population size reached, in the real world where protected areas are generally smaller than unprotected sites, density dependence is likely to be relevant. Thus, a more sophisticated density-dependent model may be more useful for assessing management policies. However, our comparative framework will be particularly effective for evaluating perturbation responses across species for which we do not have detailed information on dispersal and for those that exhibit clear changes in habitat through their life history.

Arguably, a species by species approach may have limited value when designing networks of reserves over a large ecoregion, where biodiversity protection accompanies fishery enhancement as a conservation goal. However, we believe that a representative group of species covering a wide range of life histories could be used to design a network of marine reserves at an ecoregional level. For example, the species treated here as case studies all inhabit, permanently or temporarily, the Gulf of California. In the Gulf of California, there is currently a move afoot among scientists, conservation organizations, and the Mexican government to establish new protected areas. Recent studies in the central and southern Gulf have proposed a design strategy for the establishment of such no-take reserves using data on biodiversity, ecological processes, and socioeconomic factors (Sala et al. 2002). However, there are no general formulae to decide how to prioritize establishment of reserves to maximize recovery of imperiled populations. Further, most existing reserves do not have explicit goals and expectations, and temporal changes in the species populations in the reserves are not consistently monitored. An important next step will be to use our conceptual framework as a basis for identifying relevant time frames for monitoring based on life history and dispersal data.

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PERSPECTIVE / PERSPECTIVE

Life history strategies, population regulation, and implications for fisheries management[1]

Kirk O. Winemiller

Abstract: Life history theories attempt to explain the evolution of organism traits as adaptations to environmental variation. A model involving three primary life history strategies (endpoints on a triangular surface) describes general patterns of variation more comprehensively than schemes that examine single traits or merely contrast fast versus slow life histories. It provides a general means to predict a priori the types of populations with high or low demographic resilience, production potential, and conformity to density-dependent regulation. Periodic (long-lived, high fecundity, high recruitment variation) and opportunistic (small, short-lived, high reproductive effort, high demographic resilience) strategies should conform poorly to models that assume density-dependent recruitment. Periodic-type species reveal greatest recruitment variation and compensatory reserve, but with poor conformity to stock–recruitment models. Equilibrium-type populations (low fecundity, large egg size, parental care) should conform better to assumptions of density-dependent recruitment, but have lower demographic resilience. The model's predictions are explored relative to sustainable harvest, endangered species conservation, supplemental stocking, and transferability of ecological indices. When detailed information is lacking, species ordination according to the triangular model provides qualitative guidance for management and development of more detailed predictive models.

Résumé : Les théories démographiques cherchent à expliquer l'évolution des caractéristiques des organismes comme des adaptations à la variation du milieu. Un modèle qui comprend trois stratégies démographiques primaires (les points extrêmes d'une surface triangulaire) décrit les patrons généraux de variation de façon plus complète que les méthodes qui examinent des caractéristiques individuelles ou qui se limitent à classifier les cycles biologiques en « rapides » et « lents »; il fournit une méthodologie générale pour prédire a priori les types de populations qui possèdent des degrés faibles ou élevés de résilience démographique, de potentiel de production et de conformité au contrôle lié à la densité. Les stratégies périodiques (forte longévité, fécondité élevée, importante variation du recrutement) et opportunistes (petite taille, vie courte, effort reproductif élevé, grande résilience démographique) devraient mal s'accommoder des modèles qui présupposent un recrutement relié à la densité. Les espèces de type périodique possèdent la variation de recrutement et la réserve de compensation les plus grandes, mais elles s'ajustent mal aux modèles de stock–recrutement. Les populations de type équilibré (fécondité basse, oeufs de grande taille, soins parentaux) devraient s'ajuster mieux aux présuppositions de recrutement relié à la densité, mais elles ont une résilience démographique plus faible. Les prédictions du modèle sont examinées en ce qui a trait à la récolte soutenable, la conservation des espèces menacées, le stockage d'appoint et la transférabilité des indices écologiques. Quand il manque de renseignements précis, une ordination des espèces d'après le modèle triangulaire fournit un guide qualitatif pour la gestion et la mise au point de modèles prédictifs plus détaillés.

[Traduit par la Rédaction]

Introduction

Life history theories seek to explain the evolution of organism traits as adaptive responses to environmental variation and differential mortality or resource allocation to life stages (Roff 1992; Stearns 1992). Life history theories also examine how traits are intercorrelated and constrained by ecological factors. Reproductive effort varies in relation to mortality schedules (Cole 1954; Murphy 1968; Benton and Grant 1999), and reproductive allocation to optimize off-

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K.O. Winemiller. Section of Ecology and Evolutionary Biology, Department of WFSC, Texas A&M University, 2258 TAMU, College Station, TX 77843-2258, USA (e-mail: k-winemiller@tamu.edu).

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spring size versus numbers is influenced by the scale of environmental variation (Southwood 1988), availability of resources for early life stages (Pianka 1970), or the degree of environmental stress (Grime 1977). Life history theories also predict demographic response to disturbances at variable spatial and temporal scales. For example, organisms may adopt strategies of iteroparity or migration to maximize reproductive success in variable environments (Murphy 1968; Roff 1988; Orzack and Tuljapurkar 1989).

Life history theories have been invoked to predict relative influences of density-dependent versus density-independent ecological influences on life stages and age classes (Reznick et al. 2002). The most notable example is the theory of *r*- and *K*-selection (MacArthur and Wilson 1967; Pianka 1970), in which populations possessing the *K*-selected suite of attributes (delayed reproduction, low fecundity, large parental investment in individual offspring, long life-span) are expected to have higher fitness under density-dependent influences (competition, predation) than species having the opposite suite of *r*-selected traits. Interactions among species traits, ecological influences, and population dynamics can be simulated by manipulating organism traits and ecological variables using matrix-based (e.g., Orzack and Tuljapurkar 1989; Grant and Benton 2000; Van Tienderen 2000) and individual-based models (e.g., Van Winkle et al. 1993). A limitation of these models is that variables generally are manipulated independently without knowledge of the nature of functional constraints among suites of life history traits. Species life history attributes have been examined in relation to diverse fisheries management challenges, including environmental assessment (Schlosser 1990), extinction risk (Parent and Schriml 1995; Jennings et al. 1999*b*; Reynolds et al. 2005), and resilience to harvest and other human-induced sources of mortality (Beverton 1992; Van Winkle et al. 1993; Rochet et al. 2000). My objective here is to explore fisheries management implications of a triangular model of life history evolution that identifies adaptive suites of attributes by taking into account functional constraints (Winemiller 1989, 1992; Winemiller and Rose 1992).

A model of primary life history strategies

Several models ordinate species according to patterns of life history variation. Perhaps the best known is the *r*–*K* selection model. Tests of this model seem to have yielded as much negative as positive evidence (Stearns 1992). Some of these experimental tests proposed that *K*-selection should select for larger population carrying capacity (*K*). Yet, the original *K*-selection model (Pianka 1970) merely proposed that selection in chronically resource-limited and (or) predator-rich habitats should favor certain traits, such as parental care and higher juvenile and adult survival, attained at the expense of early investment in reproductive effort and large clutches of small offspring. Another problem is that the *r*–*K* continuum fails to recognize additional axes of variation required to describe patterns of interspecific variation in nature (Winemiller 1992; Reznick et al. 2002). Several two-dimensional, triangular models of life history evolution have been proposed. Grime (1977) proposed a model for plants that contrasted ruderal (*r*-selected with high reproductive allocation), competitive (*K*-selected with greater investment in soma), and stress-resistant species (plants with traits of adults and (or) seeds that enhance fitness in harsh habitats). Attributes of stress-resistant species essentially are more extreme expressions of those defining the competitive strategy. Based largely on evidence from insects, Southwood (1977, 1988) and Greenslade (1983) proposed a triangular model of adversity selection that shares many features of the Grime model. In these models, environmental gradients of productivity and disturbance influence resource availability and stress.

Based on evidence from Pacific fishes, Kawasaki (1980) proposed a triangular model of fish life history strategies that contrasts small, early maturing species having high reproductive effort, and low batch fecundity (Type IA) with larger species possessing later maturation, longer life-spans, and high fecundity (Type II). The third strategy (Type IB) possesses attributes that are essentially intermediate. According to Kawasaki (1980), Type IA species are favored when environmental variation is "irregular" (i.e., variable in the short term), with recruitment dynamics also being irregular. Type IB species are favored when environmental variation occurs over longer periods, and Type II species are favored when environmental variation is low and predictable.

Based on patterns of life history variation in tropical freshwater fishes (Winemiller 1989) and North American freshwater and marine fishes (Winemiller and Rose 1992), a triangular model of life history evolution was proposed to explain adaptive response to environmental variation in terms of its predictability and scale relative to generation time. The Winemiller and Rose (W&R) model recognizes three endpoint strategies: (*i*) opportunistic (short generation time, high reproductive effort, small body size, low batch fecundity, and low investment per offspring), (*ii*) periodic (long generation time, moderate reproductive effort, large body size, high batch fecundity, and low investment per offspring), and (*iii*) equilibrium (moderate to long generation time, low reproductive effort, variable body size, low batch fecundity, and high investment per offspring). This model appears superficially similar to Kawasaki's (1980) model; however there are major differences. Kawasaki's Type IA blends attributes of opportunistic (short life-span, high reproductive effort, high *r*) and equilibrium (slow growth rate, large eggs, parental care) endpoint strategies. Kawasaki's Type IB strategy is a mixture of equilibrium (intermediate age of maturity, low fecundity, low *r*) and periodic (long life-span, high growth rate) endpoints. Kawasaki's Type II strategy corresponds to the periodic strategy, but his model proposes that stable and predictable habitats select for this suite of attributes, whereas the W&R model proposes adaptation in response to large-scale periodic variation in space or time.

Each endpoint strategy in the W&R model can be viewed as an adaptive suite of attributes associated with maximizing the per capita rate of population increase, *r*, according to the demographic relationship $r = \ln(\Sigma l_x m_x)/T$, where l_x is age-specific survivorship, m_x is age-specific fecundity, and T is generation time. This relationship actually defines a set of life history trade-offs (Laughlin 1965; Southwood et al. 1974; Kawasaki 1980). Relative investment in tissues–activities that increases survivorship also reduces lifetime fecundity (greater allocation to soma and maintenance functions reduces alloca-

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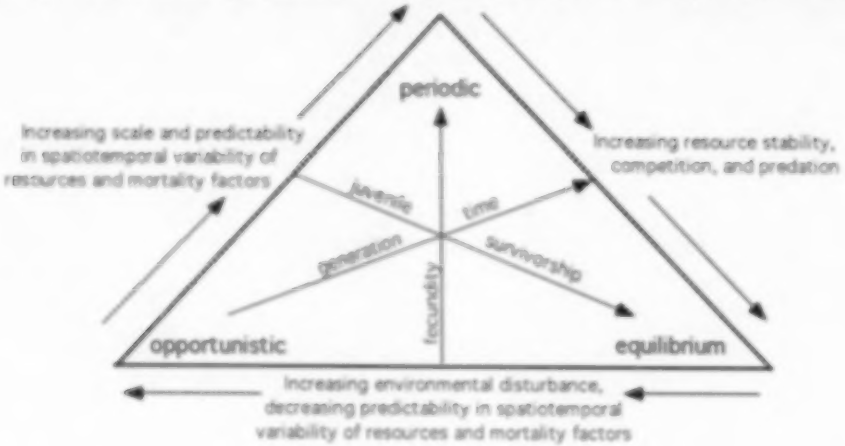
Fig. 1. Triangular life history model illustrating environmental gradients selecting for endpoint strategies defined by optimization of demographic parameters generation time (T), age-specific survivorship (l_x), or age-specific fecundity (m_x) (from Winemiller 1995).



tion to gametes and associated reproductive tissues and functions) and increases generation time (greater investment in somatic growth prior to maturation increases the interval to maturation). Larger reproductive allocation in the form of greater fecundity would reduce survivorship (given lower relative investment in soma and maintenance processes) and would increase generation time (high fecundity can be achieved only by delaying reproduction until a sufficiently large size has been attained). Reduction in generation time as a means to increase r would reduce both survivorship (because reproduction takes place sooner with less investment in soma and maintenance) and fecundity (because earlier maturing organisms are smaller with less biomass and energy available to produce large clutches of eggs). The result of these functional trade-offs is a species ordination according to suites of life history traits that defines an adaptive surface within the space defined by juvenile l_x, m_x, and T (Winemiller 1992; Winemiller and Rose 1992).

Environmental gradients likely to select for each endpoint strategy are outlined (Fig. 1). Given other factors held constant, the intrinsic rate of increase is more sensitive to changes in generation time than to changes in fecundity or survivorship (Lewontin 1965). Thus, the opportunistic suite of attributes could be considered a colonizing strategy that should maximize fitness in environmental settings dominated by density-independent, ecological influences. Such conditions might be expected in productive habitats subjected to frequent and intense disturbances, such as ephemeral pools, intermittent streams, and salt marshes. Indeed, these habitats often are dominated by species, such as poeciliids (livebearers) and fundulids (killifish), with generation times of only a few months.

The periodic strategy maximizes fitness when environmental variation influencing early life stage survival is periodic (relatively predictable) and large scale (Winemiller and Rose 1992, 1993). In a sense, the periodic strategy could be considered an intergenerational form of bet-hedging, whereby reproductive effort is distributed over several reproductive bouts when variation in juvenile survival is greater than variation in adult survival. By allocating reproductive output across multiple years, some individuals achieve reproductive success despite long intervals with environmental conditions unfavorable for early life stage survival. The periodic strategy seems to be the dominant strategy observed in fishes, arthropods, mollusks, and plants (Winemiller 1992), which probably reflects ubiquitous large-scale spatial (patchiness) and temporal (seasonality) heterogeneity of ecosystems. Temperate and tropical lotic ecosystems are seasonal, and tropical marine systems are characterized by spatial heterogeneity over large scales (e.g., convergence zones, gyres, coastal currents, and coastal depth and salinity gradients) or are subject to climatic events such as storms and El Niños. Large-scale environmental variation is believed to drive variation in early life stage recruitment for periodic-type marine fishes (e.g., Kawasaki 1985; Hedgecock 1994; Gilbert 1997).

The equilibrium endpoint is essentially the K-selected strategy of high investment in soma and individual offspring at the expense of maximizing per capita growth via reduction of generation time or increases in fecundity. This strategy is a comparatively inefficient means of maximizing the intrinsic rate of increase and appears to be favored in environmental settings having chronic or frequent density-dependent influences (K-selection) or in stressful habitats (adversity selection). The equilibrium strategy is common among fish taxa inhabiting caves (e.g., branchial-brooding amblyopsids), tropical lakes (e.g., mouth-brooding cichlids), and coral reefs (e.g., brood-bearing syngnathids, live-bearing elasmobranches). It is important to keep in mind that diverse life history strategies may be present among species inhabiting a single habitat (Winemiller 1989). Species with different ecological niches, body sizes, anti-predator defenses, etc., perceive and respond to components of environmental variation in different ways. For example, a large-bodied species, such as a sciaenid, may migrate between an estuary and coastal waters in response to spatial and seasonal variation in food resources and abiotic conditions at the landscape scale. These periodic strategists produce large batches of small eggs that disperse passively and yield high recruitment under appropriate environmental conditions that occur once a year or perhaps even once a decade. In contrast, small

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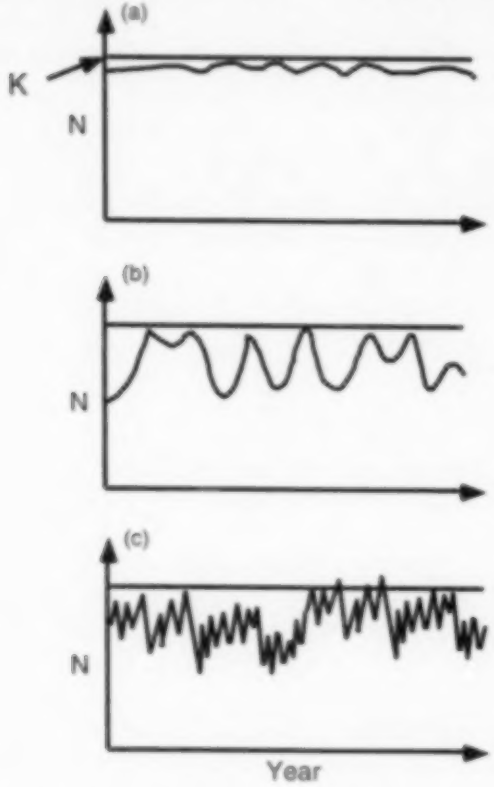
Fig. 2. Predicted population dynamics in relation to a hypothetical carrying capacity (K) imply the relative strength and frequency of density dependence. (*a*) Equilibrium-type population; (*b*) periodic-type population; (*c*) opportunistic-type population.



killifish in the same estuary are restricted to shallow marginal habitats at a local scale. High variance in abiotic (water depth and quality) and biotic (food and predator densities) conditions imposes high and often unpredictable mortality on both juveniles and adults of these relative opportunistic strategists.

The triangular model of life history evolution was derived from interspecific comparisons and therefore predicts general relationships. Nonetheless, the model's adaptive surface recognizes fundamental constraints. Other aspects of life history variation can be examined in addition to these primary demographic strategies. For example, Balon (1975) defined reproductive guilds based on spawning behavior and specific environmental needs of early life stages. The triangular model qualitatively predicts population responses in relation to a hypothetical carrying capacity, which implies the relative strength or frequency of density dependence influencing population regulation. Here, density dependence includes behavioral, physiological, and demographic responses to predators and interspecific competitors, as well as intraspecific resource competition. Populations of opportunistic strategists would be expected to be well below K most of the time and frequently subject to density-independent sources of mortality (Fig. 2). Periodic strategists should show greater interannual recruitment variation than equilibrium strategists, the latter having relatively low variation with mortality and reproductive success being more strongly influenced by density-dependent influences (Fig. 2). During occasional years of high recruitment, periodic strategists may reach densities that lead to significant density-dependent responses in growth and survival, especially among immature age classes. In long-lived periodic strategists, unusually strong annual cohorts may dominate the adult population for many years. Large spatial variation in environmental conditions can yield large intra-annual variation in recruitment success (Hedgecock 1994), and larger fishes with high fecundity may contribute disproportionately to recruitment (Berkeley et al. 2004). Such patterns are predicted to be weaker for species with opportunistic and equilibrium-type life history strategies.

Is recruitment variation greater for populations with the periodic strategy and lower for populations with the equilibrium strategy? One way to test this hypothesis is to plot recruitment variation (coefficient of variation for annual recruitment) as a function of batch fecundity for a group of related species (i.e., high batch fecundity distinguishes the periodic strategy). A strong relationship is revealed between recruitment variation and fecundity for North American freshwater perciforms (Fig. 3), a group that spans a broad spectrum of strategies. In this data set, all of the low-fecundity species are associated with the equilibrium strategy (delayed reproduction, large egg size, parental care), so that fecundity alone contrasts an equilibrium–periodic gradient. Among North American freshwater perciforms, periodic strategists tend to have higher interannual recruitment variation than equilibrium strategists. Mertz and Myers (1995) found no relationship between the standard deviation of log(recruitment) versus log(fecundity) for 41 marine and anadromous fish species. Analyses performed by taxonomic orders yielded weak positive but statistically nonsignificant relationships. Most of the species in their data set were positioned far to the periodic end of the spectrum (fecundities ≥ 15 000), and only a single example positioned near the equilibrium endpoint was included (*Squalus acanthias*, fecundity = 3). Rickman et al. (2000) found higher fecundity was significantly associated with higher recruitment variation for 13 of 14 comparisons among exploited marine stocks. When this analysis was repeated without regard for evolutionary relatedness, the trend was not statistically significant.

Stock–recruit (S–R) relationships provide an effective means to view compensatory density dependence in population regulation. The strength of empirical fit to the S–R model indicates the degree to which recruitment is explained by stock density. In theory, the empirical fit should be strong for species with extreme forms of the equilibrium life history strategy and poor for species having opportunistic and periodic attributes (Fig. 4). Moreover, the shape of the S–R curve predicts the manner in which the population responds to variation in stock density, and species with different life history strategies logically should respond differently. Compensation potential, or the capacity for a population to respond rapidly to density-dependent changes at low population abundance, is indicated by the steepness of the slope of the Ricker S–R curve near the origin (Myers et al. 1999; Myers 2001). Rose et al. (2001) grouped 249 populations from the S–R database of Myers et al. (1999) (http://fish.dal.ca/~myers/data.

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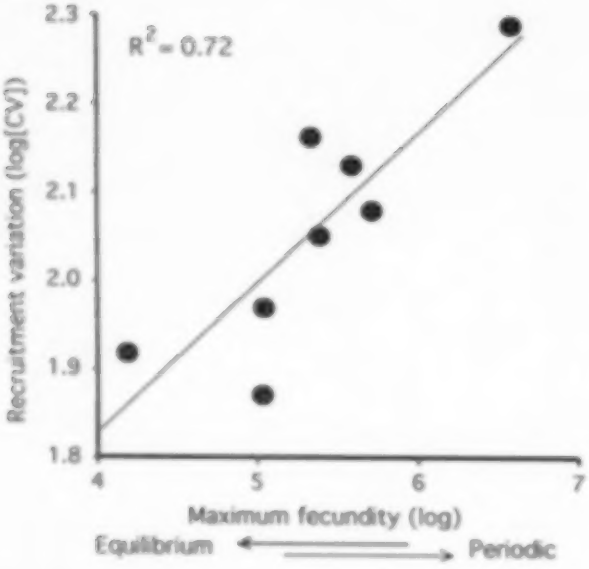
Fig. 3. Plot of recruitment variation as a function of fecundity for North American freshwater perciforms (centrarchid and percid data from R.A. Myers' stock–recruitment database, http://fish.dal.ca/~myers/data.html; when multiple databases were available for a species, only the longest time series was analyzed).



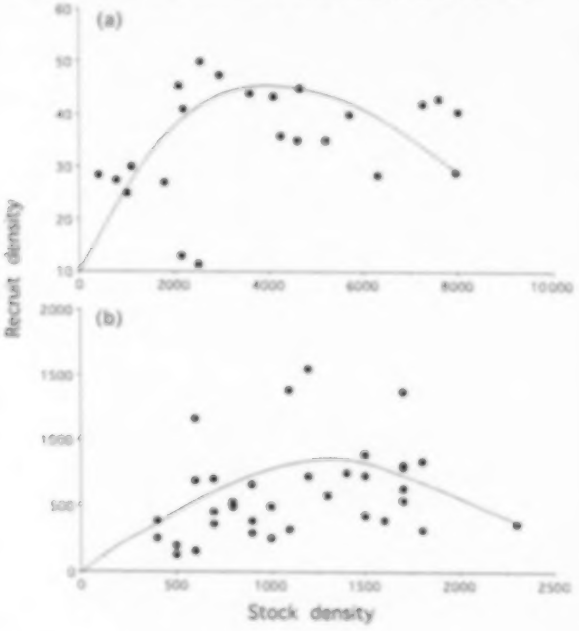
html) according to life history strategies and examined the mean compensation potential (steepness) for each group. As hypothesized, periodic species tended to be associated with a steeper slope than equilibrium and opportunistic strategists. In addition, equilibrium strategists tended to have lower residual variation in fits to S–R relationships, but variance around mean values was high for all three groups. It should be noted that none of the species in this dataset could be considered extreme forms of the opportunistic or equilibrium strategies. An extreme example of the equilibrium strategy would be mouthbrooding and substrate-nesting cichlids of the African rift lakes. For example, several *Lamprologus* species of Lake Tanganyika are entirely dependent on empty snail shells for refuge from predators and for nesting (Konings 1998), and it is likely that shell availability determines population size.

The remainder of this perspective will explore implications of the triangular life history model for fisheries management. I will briefly cover four general issues: (*i*) sustainable harvest, (*ii*) conservation of rare and threatened species, (*iii*) stock enhancement via supplemental stocking, and (*iv*) equilibrium assumptions of ecological indices. Other issues, including marine reserves and invasive species, also could profit from insights gained by life history theory, but space limitations restrict discussion of those topics.

Sustainable harvest

The traditional view of sustainable harvest was well expressed by McFadden (1977): "Experience with the world's major stocks has proven both that they have the capacity to withstand impressively high levels of exploitation and produce substantial surplus at population levels well below their pre-exploitation abundance, ...". This view carries the implicit assumption of density compensation to sustain a population under harvest. The degree to which r is elevated, via compensatory adjustments in population birth (b) and death (d) rates, above replacement level ($r = 0$) defines harvestable surplus yield.

Fig. 4. Examples of data scatter around Ricker stock–recruit relationships. The plot in (*a*) is for a relative equilibrium strategist, brown trout (*Salmo trutta*) from Black Brows Beck, English Lake District (Elliot 1994), in which stock abundance is the number of fertilized eggs per 60 m^2 and recruit abundance is the number of age-1+ fish per 60 m^2 (coefficient of determination = 0.21). The plot in (*b*) is for a relative periodic strategist, pike (*Esox lucius*) in South Windermere Lake, English Lake District (Kipling 1983), in which stock abundance is kilograms of mature females and recruit abundance is total number of age-2 fish.



Stock–recruit models have been used extensively in fisheries management to provide a basis for estimating density compensation, maximum or optimal sustainable yield, and biological reference points. This equilibrium view of population dynamics has long been questioned (e.g., Andewartha and Birch 1954; Fletcher and Deriso 1988; Hixon et al. 2002). Because stock–recruitment time-series data are not independent, any persistent cause of low recruitment will result in reduced spawning-stock abundance (Gilbert 2002). In such instances, analyses would yield the erroneous appearance that low spawning-stock abundance yields low recruitment. As noted previously, empirical data generally provide very poor fits to S–R models (Myers et al. 1990; Rose et al. 2001). In these instances where environmental variation has a strong influence on recruitment dynamics, sustainable-yield targets derived from S–R models provide an unsound basis for management. Exceptional cases might involve equilibrium strategists in relatively small, closed ecosystems

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(e.g., trout residing in a stream pool, or sunfish in ponds as per the Swingle paradigm discussed below). Christensen and Goodyear (1988) and Hilborn and Walters (1992) discussed potential sources of bias in S–R analyses and quantitative methods for evaluating them, such as time-series analysis of model residuals. They cautioned that management strategies targeting constant stock abundance will not be appropriate in most cases. They also contended that analyses should focus on catch variability just as much as the average catch. Koslow (1992) examined the influence of fecundity and variance in natural mortality during the pre-recruit period on characterization of S–R relationships with strong and weak density dependence. Because small variation in early vital rates result in large changes in population dynamics, simple deterministic S–R models are not applicable to fishes with high fecundity and small egg size (periodic strategists), yet such species comprise the great majority of commercial fish stocks.

Management of most of the world's large commercial fisheries is confronted with "the recruitment problem". What factors and mechanisms limit recruitment at various intervals of the life cycle? For periodic-type species, small differences in mortality of early life stages have huge potential to influence stock abundance. A variety of exogenous factors (e.g., abiotic environmental variation, fluctuations in food supplies or predator densities) are implicated (Cushing 1990; Leggett and DeBlois 1994; Myers 1998). The predictive capability of a stock–recruitment model for American shad increased from 3%–90% when abiotic factors were introduced (Crecco et al. 1986). Fromentin et al. (2001) analyzed 136 time series of juvenile cod and concluded that populations are regulated by an interaction between density-dependent mechanisms and stochastic abiotic factors. Thus, prediction of population dynamics of periodic strategists is confronted by two fundamental problems. Variance in early life stage abundance is almost impossible to estimate with the precision necessary to make even crude population projections, and key abiotic driving variables are difficult to estimate over all but the shortest of time intervals. Large uncertainty is an unavoidable reality for quantitative projections involving periodic-type species, but stochastic models at least can permit managers to assign broad confidence limits around target values (Lande et al. 2003).

In contrast with species near the periodic endpoint, equilibrium and opportunistic strategists should have population dynamics affected by factors influencing later life stages just as much as those influencing early stages. However, these influences should be more density dependent for species with equilibrium life history attributes. For example, both the reproductive success of males and over-winter survival of age-0 smallmouth bass (*Micropterus dolomieu*) at high latitudes is strongly influenced by foraging success and growth during the preceding summer and fall (Shuter et al. 1980; Wiegmann et al. 1992). All populations are subjected to density-dependent population regulation, but the key issue is the relative strength and frequency of these influences. A statistical analysis of diverse taxa with opportunistic life histories showed strongest density-dependent changes in vital rates at low population levels (Stubbs 1977), whereas density-dependent changes were stronger at population levels near carrying capacity for mammals and birds, two groups that tend to be affiliated with the equilibrium endpoint strategy (Fowler 1981). Guppies (*Poecilia reticulata*) have extreme opportunistic history attributes (early maturation, high continuous reproductive effort); yet detailed experimental research in Trinidad has yielded evidence of interactions among population density, predation level, and food availability (Bronikowski et al. 2002).

Few equilibrium-type fishes are targets for commercial fisheries, and S–R models generally have not been applied to these species. Management methods for sportfishes in small lakes in North America pertain to circumstances in which an assumption of strong density-dependent regulation is probably valid. Small temperate lakes are closed systems with low biological diversity and relatively simple food webs. The Swingle (1956) paradigm of pond management relies on manipulation of predator and prey populations to achieve a balanced community in which individual growth rates are maximized and population fluctuations are minimized. Over the past 50 years, the Swingle paradigm has been developed into a fairly standard technology that has yielded satisfactory results in many regions of the United States, particularly in the South and Midwest (Willis et al. 1993). This technology essentially consists of stocking one or a few species of predator and prey at prescribed densities (Flickinger and Bulow 1993). Fish growth rates, condition, and population size structure are periodically monitored to determine the degree to which predator or prey populations may be showing signs of density-dependent responses to overcrowding and food limitation. The goal is to achieve a balance in the size ratios and densities of predator and prey populations (proportional stock densities).

Why has the technology for managing small lakes succeeded while more extensive efforts to manage the world's commercial marine stocks have been generally viewed as failures? Again, we must recognize that lakes are small, closed ecosystems with few species. This characteristic permits greater relative control over system components, but just as importantly, it greatly simplifies predictions regarding mechanisms controlling population dynamics. It is probably no accident that the Swingle paradigm employs equilibrium-type species for small lake management; sunfishes (Centrarchidae) are recommended as prey for black bass (Centrarchidae) or channel catfish (Ictaluridae). All of these species are substrate-nesting brood guarders with life history strategies that should be largely consistent with assumptions of strong density dependence for both juvenile and adult life stages. Similar success has been achieved in management of small lakes in South Africa using brood-guarding tilapia as prey and brood-guarding haplochromine cichlids (*Serranochromis* spp.) as predators. In South America, small lakes generally are stocked with nonindigenous tilapia as forage for brood-guarding peacock cichlids (*Cichla* spp.).

In contrast with species employed in small lake management, most of the species involved in the large commercial fisheries of the world are periodic strategists, usually in an extreme form. These populations should conform poorly to predictions of density-dependent equilibrium dynamics. To a great extent, forecasting of stock dynamics means predicting recruitment dynamics in response to large-scale abiotic drivers, most of which are highly unpredictable. Moreover, these commercial species inhabit large, open ecosystems, such as

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oceans, estuaries, large lakes, and floodplain rivers. These systems are heterogeneous, dynamic, and biologically diverse, all of which contribute to more complex interrelationships among variables influencing stock dynamics. This problem is now widely recognized, yet stock management is too often based on strong assumptions of density compensation. Williams and Shertzer (2003) recently analyzed the sensitivity of commonly used biological reference points to life history variation captured by scale invariant parameters (sensu Charnov 1993; Charnov et al. 2001). They found that biomass-based reference points were relatively insensitive to life history variation, but a mortality-based reference point was highly sensitive. Moreover, they cautioned that all of the biological reference points were sensitive to the choice of S–R function and the assumed level of population growth at low density (i.e., steepness), which renders universal reference values untenable.

So what should we do? In his last publication, Ray Beverton (1998) provided advice for managing exploited fish stocks in the face of inherent uncertainty. In the short term, we can forecast and track oncoming year classes. For the long term, objectives and targets should be reviewed frequently for medium- and long-lived species, and given our inability to make precise predictions to guide sustainable exploitation, fisheries should not overcapitalize. Beverton's advice, although general, provides a basis for developing more sophisticated means of setting and revising targets following the precautionary principle and adaptive management (Hilborn and Walters 1992). Rose et al. (2001) reviewed density compensation in fish populations and concluded that estimates of density compensation will remain controversial unless underlying mechanisms are understood to some degree. They advocated an approach that integrates life history theory, process-level understanding of mechanisms, analysis of field data, and individual-based simulation modeling. Such efforts require considerable time and resources. In the absence of detailed information, ordination of species according to the triangular life history model allows for rapid, qualitative assessments to guide management as well as research designed to efficiently fill information gaps.

Rare and threatened species

Qualitative predictions from life history theory can greatly assist management strategies for rare and threatened species. In many countries, a prime directive in most regulations designed to protect endangered species is a requirement to limit the take of rare species. Take can be construed as removal or killing of individual organisms, but it also includes indirect means of removal, such as injury or impairment to organisms or essential habitats that support their survival and reproduction. Conservation of rare species by limiting their take implies that each individual in the population is valuable in the sense that its removal will lead to further decline in numbers. In other words, compensatory density dependence is assumed to be very weak.

An assumption of weak or no density compensation is likely not true in many cases, and equilibrium-type species, in particular, are expected to exhibit strong density dependence. Even the large influence of stochastic, abiotic factors on recruitment dynamics of periodic species does not preclude influence from density-dependent ecological factors. For example, Myers and Barrowman (1996) analyzed 364 S–R time series and found significant relationships between spawner abundance and recruitment levels when a sufficiently broad range of spawner abundances was encompassed. Thus, an important issue for conservation of endangered species is to determine for which species and under what circumstances compensatory mechanisms facilitate population resilience. At low population size, compensatory factors may be cancelled by effects of inbreeding or enhanced sensitivity to environmental variation. Population turnover rate is another key factor that influences resilience. Larger species have longer generation times and greater vulnerability to exploitation because they possess lower potential rates of population increase (Winemiller and Rose 1992; Jennings et al. 1998, 1999*a*).

What are the attributes of endangered species relative to the triangular model of primary strategies? Review of the current US Fish and Wildlife Service list of 116 fish species listed as threatened or endangered reveals some striking patterns. First, 102 species (88%) are freshwater fishes, 10 species (9%) are anadromous, and 4 species (3%) inhabit nearshore coastal habitats. Freshwater habitats and watersheds have been greatly perturbed, including introductions of invasive nonindigenous species. The status of rare marine species has not yet been assessed to the same extent as freshwater fishes, but even so, impacts on freshwater fishes seem to be particularly serious (Harrison and Stiassny 1999).

Second, 82 species (71%) are small (maximum standard length <15 cm). This percentage of small fishes is greater than the percentage based on the native North American freshwater fish fauna as a whole (64%, based on data compiled by Lee et al. 1980), but not significantly greater (χ^2 = 1.12, df = 2, P = 0.29). Third, 46 endangered species (40%) can be classified as opportunistic species (maturity ≤1 year, high reproductive effort often with multiple spawning bouts), 42 species (36%) are periodic strategists (maturity ≥1 year, high fecundity often with pulse spawning), and only 28 species (24%) are equilibrium strategists (relatively large eggs, parental care). Percentages for the continental freshwater fish fauna (estimated in the same manner using information from Lee et al. 1980 and regional fish compendia) are 30% (opportunistic), 54% (periodic), and 17% (equilibrium). Thus, opportunistic and equilibrium-type species tend to be disproportionately threatened (χ^2 = 4.64, df = 2, P = 0.098).

The observation that more than two thirds of endangered fishes have relatively opportunistic life histories yields an apparent paradox, since these populations should possess a high degree of demographic resilience (low generation times and high reproductive effort yielding high intrinsic rates of increase). But the paradox is solved when one considers the specific circumstances threatening these species. Most of these species occur either in relict habitats in the arid southwestern United States (e.g., *Cyprinodon* and *Gambusia* spp.) or in relatively isolated headwater streams in the southeastern United States (e.g., *Notropis*, *Noturus*, and *Etheostoma* spp.). Small desert fishes are endangered because they are the last survivors from a fauna that was once more diverse during mesic conditions of the past (Smith et al. 1995). High demographic resilience has allowed them to persist in the face of extinctions of species requiring larger and more sta-

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ble or predictable habitats. The desert pupfish (*Cyprinodon macularius*) provides a good example. The only remaining population survives in an isolated pool in the Death Valley Basin. Prior to the Pleistocene, the basin received water from extensive drainage systems in the surrounding uplands, but today it is one of the driest places on earth. The species continues to survive with a precarious foothold in a water-filled limestone cavern measuring 3 m × 6 m. Human intervention has managed to stave off extinction of the desert pupfish (Ono et al. 1983). Similarly, populations of opportunistic-type fishes in southeastern streams also should be highly resilient, provided there are refugia from which individuals can reinvade habitats following disturbances. These species frequently are threatened by total habitat destruction (hydrologic alteration, siltation, and pollution) and invasive species.

A second general grouping of threatened fishes identifies relatively large, periodic strategists, the type of life history that should show high recruitment variation with low conformity to density-dependent recruitment expectations, yet also have highest compensatory potential. Endangered periodic fishes fall into two groups: anadromous species and species that inhabit large rivers, mostly in the western United States. Migratory behavior tends to be associated with extreme forms of the periodic strategy (Winemiller and Rose 1992), and a major impact on populations of these fishes is dams and degradation of instream habitats and watersheds. Many of these threatened periodic species migrate long distances to complete their life cycles (e.g., anadromous salmonids and sturgeons), and others use multiple habitats in large rivers during different life cycle stages under variable hydrological conditions (e.g., large cyprinids and catastomids).

The remaining threatened fishes have equilibrium-type life history attributes, which should conform better to predictions of density compensation. These include spring-dwelling fishes (e.g., *Prietella phreatophila*, *Speoplatyrhinus poulsoni*) and trout endemic to small drainage basins of the West (e.g., *Oncorhynchus aguabonita whitei*, *Oncorhynchus clarki seleniris*). Clearly, these fishes are endangered by loss of habitat. The basic issue is not that populations lack resilience or compensatory potential and thus cannot sustain some degree of mortality or take. The problem is loss of habitat or the ecological basis for density compensation. Thus, equilibrium-type species should be resilient to anthropogenic mortality, especially for juvenile life stages, but highly sensitive to habitat loss or degradation. For long-lived equilibrium strategists, such as sharks, the most serious problem is the lack of demographic resilience due to low natural rates of recruitment, long generation times, and low population turnover rates. Sensitivity to harvest by *K*-strategists with long recovery times has been demonstrated many times (e.g., Lewontin 1965; Adams 1980), and the plight of sensitive elasmobranch populations is gaining increasing attention (Musick et al. 2000).

Parent and Schriml (1995) analyzed a suite of 18 life history and 31 ecological variables for fishes of the North American Great Lakes to derive logistic regression models to predict whether or not species were at risk of extinction. The life history variables with greatest contributions to the model were age of maturity and life-span, and dominant ecological variables tended to be associated with spawning and feeding substrates, especially in streams. They inferred that species maturing at 18 years or greater (in this region, these long-lived species tend to be periodic-types such as sturgeons) faced greatest extinction risk; however, it should be noted that relative to the continent as a whole, the Great Lakes region of North America does not contain a very large number of rare endemic species in relict habitats. Nonetheless, the multivariate statistical approach employed by this study would aid risk assessments of vulnerable species in other regions of the world.

Supplemental stocking of marine fishes

Supplemental stocking has long been a mainstay of fisheries management in freshwater systems. Lakes and impoundments are stocked annually by government agencies to enhance sportfishing, and cool-water streams are stocked with trout to enhance fishing opportunities. In small aquatic systems, there is a high probability that fish stocked at sufficiently large size will eventually be harvested by anglers. In small systems, overstocking can cause adverse density-dependent responses in terms of reduced individual growth rates and reproductive success. Stocking to supplement wild populations in large open ecosystems, especially marine waters, is more controversial (Grimes 1998). Anadromous species have been stocked for decades in areas where dams have impeded migrations to spawning grounds. In the United States, this practice has been essential for preserving local stocks of anadromous salmonids, although perhaps not without risk of deleterious genetic effects. Some regions have initiated supplemental stocking programs for marine species in which millions of fry or juveniles are released into coastal waters in efforts to augment wild populations. Many of the species involved in these programs are periodic strategists in an extreme form. For example, each year state agencies in Florida and Texas release millions of hatchery-reared red drum, *Sciaenops ocellatus*, into bays and estuaries of the Gulf of Mexico. The red drum has a long life-span and extremely high fecundity accompanied by high early mortality yielding high fitness variance (Turner et al. 2002). More importantly, the species displays extremely high variance in natural recruitment. Scharf (2000) analyzed a 20-year data set for juvenile red drum from nine estuaries along the Texas Gulf coast and found that intermittent occurrence of strong year classes was positively correlated across estuaries. This pattern is consistent with the notion that large-scale climatic and oceanographic factors govern early life stage survival and year-class strength in this species. Scharf also discovered evidence suggesting density dependence affecting age-0 survival, but he was unable to detect effects of a decade of stocking fingerlings on the abundance of age-0 or age-1 red drum.

Under all but the most unusual circumstances, supplemental stocking of early life stages is unlikely to translate to enhanced adult stocks for fishes with the extreme periodic strategy. During periods of poor natural recruitment, fishes stocked at a sufficiently large size might enhance coastal populations. In most cases, the numbers required to achieve this effect would be cost prohibitive. During years of strong natural recruitment, supplemental stocking would have virtually no impact on population dynamics. Under optimal conditions for early life stage survival, growth, and development,

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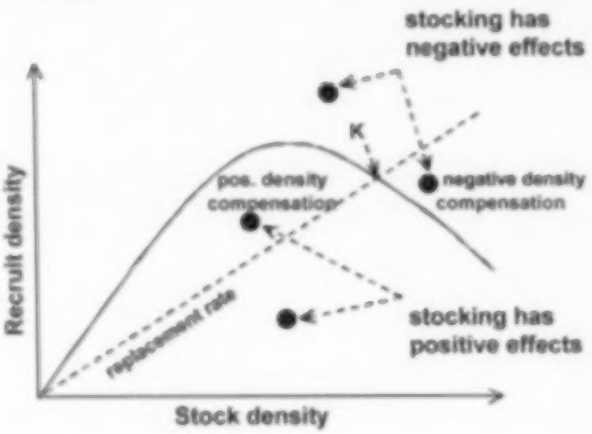
egg production from the wild spawners would swamp out hatchery production. Populations of periodic strategists frequently are dominated by occasional strong year classes.

Potential positive and negative effects of supplemental stocking can be illustrated in an S–R diagram (Fig. 5). If the population is below carrying capacity, then stocking will have positive effects on recruitment, but the amount of benefit depends on the production (trophic) capacity of the ecosystem. In diverse communities with complex food webs, competing species might have enhanced recruitment or growth from available resources during years of low natural recruitment by the target species. During years of high natural recruitment, supplemental stocking would increase the intensity of competition. Given that most years are predicted to be suboptimal for recruitment, this scenario in which stocking yields negative effects should be fairly infrequent. Nonetheless, the high cost associated with supplemental stocking of periodic-type marine fishes would be difficult to justify given doubtful benefits in terms of harvestable stocks. Of course, there could be indirect ecological benefits from stocking even during years of high natural recruitment, such as supplementing the food supply for piscivores; however, this is not likely to be a management objective. Supplemental stocking could be important for populations in which natural production has been effectively eliminated by anthropogenic causes (e.g., dams blocking spawning migrations of salmon or decimation of spawning aggregations of groupers on coral reefs).

Fisheries managers in Texas are examining the potential for supplemental stocking programs to enhance tarpon, *Megalops atlanticus*, a popular marine sportfish that has declined in Texas coastal waters in recent decades. Tarpon are extreme periodic strategists, with maturation at about age 10, a life-span of over 50 years, and batch fecundities from 1 to 20 million (Crabtree et al. 1997). As tarpon pass from a leptocephalus larval stage into the juvenile stage, they enter coastal passes and reside for variable periods of time in coastal wetlands before returning to the sea. Recruitment into wetlands varies between years and is strongly influenced by climate and coastal currents (Shenker et al. 1995). Winemiller and Dailey (2002) developed an age-based matrix model of tarpon to simulate effects of environmental variation and stocking larvae or juveniles of different ages on adult stock abundance. Only stocking huge numbers of juveniles resulted in relatively modest increases in adult stocks. When density dependence was introduced into simulations, the benefits of stocking were eliminated. Simulation of stochastic interannual variation in larval survival had a vastly greater effect on the population than either density dependence or stocking.

Supplemental stocking of opportunistic-type species generally is not practiced in large open ecosystems. In part, this is because most of these small fishes have low economic importance as harvested stocks. But this also may be due to the implicit realization that these fishes tend to have high adult mortality, short life-spans, high population turnover, and high demographic resilience. The fishes that likely would respond best to supplemental stocking are the equilibrium strategists, but would there be benefits in marine systems? Perhaps so, if the population was sufficiently depleted and restricted to a limited region or habitat. Sharks and other elasmobranches inhabiting coral reefs or estuaries might benefit from supplemental stocking. This is because the natural rate of recruitment, population turnover, and demographic resilience are low. Thus, elasmobranches rank among the most vulnerable marine fishes, and many populations show signs of depletion (Musick et al. 2000). Supplemental stocking of sharks and rays has not been explored, probably because of limited direct economic incentives and high cost that would surely be associated with captive rearing.

Fig. 5. Hypothetical stock–recruit model illustrating regions in which supplemental stocking would have positive (pos.) or negative effects.



Equilibrium assumptions of ecological indices

A variety of indices are used for assessment of the status or relative health of fish populations and aquatic ecosystems. Allocation of limited freshwater supplies is a major issue globally, and assessment of instream flow needs for aquatic ecosystems is a major fisheries management challenge (Poff et al. 1997; Richter et al. 1997). Many instream flow methodologies for protection of lotic systems assume that microhabitat availability controls fish populations (Fausch et al. 1988; Stalnacker 1993; Hardy 1998), but this assumption of density dependence probably is not true for most species most of the time. According to Orth (1987), "microhabitat availability is not the only factor limiting fish populations and does not operate continuously". Thus, we are again confronted with the challenge of determining the species and environmental settings subject to density-dependent mechanisms of population regulation. Schlosser (1990) noted that fishes inhabiting upstream reaches of temperate streams tend to be smaller with shorter life-spans and earlier maturation than downstream species. He characterized upstream populations as rapid recolonizers of habitats following severe physical disturbances, such as scouring floods or drought. He concluded that high temporal variability of fish assemblage structure in upstream reaches makes it difficult to apply fish-based indices for assessment of subtle changes in ecosystem status due to anthropogenic disturbances. Citing similar issues, Grossman et al. (1995) concluded that "although we

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should not ignore studies of the physical habitat requirements of ESUs [evolutionarily significant units], it is likely that the development of more biologically realistic, mechanistic models of habitat selection will facilitate the preservation and management of these fishes".

Transferability of habitat suitability criteria (HSC) used for instream flow assessments is an issue that life history theory can guide. Freeman et al. (1997) examined HSC relationships with depth, velocity, substrate type, and cover for nine fish species in four unregulated streams of the piedmont and coastal plains in the southeastern United States. Indices were then tested for transferability between the four study sites plus an additional regulated river. HSC transferred reasonably well for three percid species largely restricted to riffle habitats. Tests of HSC transferability failed or were inconsistent for the other six species that commonly occupied a range of pool and riffle habitats. The six habitat generalists were mostly species that lie between the opportunistic and periodic regions of the triangular continuum (three *Cyprinella* spp., two *Percina* spp., *Etheostoma stigmaceum*). The riffle species were *Etheostoma jordani*, *Etheostoma chuckwachatte*, and *Percina palmaris*, species with lower batch fecundities and tending to be positioned between the opportunistic and equilibrium regions of the continuum. Riffles are structurally complex habitats dominated by small species with opportunistic or equilibrium-type characteristics. Equilibrium-type species, such as darters (Percidae), sculpins (Cottidae), and madtoms (Ictaluridae) in North America and armored catfishes (Loricariidae) in South America, frequently occupy microhabitats under or near rocks that provide protection from swift currents as well as from predators. Abundances of these populations may be influenced by the availability of suitable microhabitats. For example, Baltz et al. (1982) demonstrated competition for riffle microhabitats among speckled dace (*Rhinichthys osculus*) in a California stream, and Petty and Grossman (1996) found that habitat use by mottled sculpin (*Cottus bairdi*) in an Appalachian stream was associated with patterns of food availability.

Indices of biotic integrity (IBIs) have become important tools for rapid ecological assessment of streams (Karr et al. 1986). IBIs infer a normal or ideal community structure that should occur in an unimpacted habitat. A numeric scale of overall ecological health is generated by summing values from a series of scaled factors, such as the percentage of species intolerant to degraded water quality and the percentage of species that are top carnivores. Because they can provide relatively rapid and inexpensive ecological assessments, IBIs have been adopted by natural resource agencies worldwide. Yet little research has been conducted to determine the mechanisms that determine population and community structure, such that the conditions that create a normal community are usually not understood. This lack of understanding about processes and mechanisms is overcome by using reference sites as means of calibrating the IBI scale to the ideal or unimpacted context.

Stream fish communities are known to respond to a variety of abiotic and biotic factors that vary stochastically or periodically on different temporal and spatial scales (Horowitz 1978). Fish assemblage structure in an Appalachian stream was more strongly associated with hydrological variation than with biotic variables indicative of species interactions (Grossman et al. 1998). In a 10-year study of a California stream, discharge differentially influenced year-class strength and relative abundances among species with different life history strategies (Strange et al. 1992). Assemblage structure in a tropical lowland stream was associated with both abiotic and biotic factors that varied with wet–dry seasonality (Winemiller 1996*a*). Life history strategies influenced species responses to environmental fluctuations and biotic interactions (Winemiller 1989, 1996*a*). Similar patterns and associations have been described for other low-gradient systems in tropical (Ponton and De Mérona 1998; Mérigoux et al. 1999; Petry et al. 2003), subtropical (Kushlan 1976), and temperate (Winemiller 1996*b*) regions. In short, opportunistic strategists would be expected to show rapid responses to habitat disturbance and domination of habitats subjected to relatively frequent and stochastic patterns of disturbance. Periodic-type species should dominate habitats with larger-scale and more predictable patterns of environmental variation, such as large floodplain rivers and estuaries. Equilibrium-type species should be favored in stable habitats (e.g., tropical lakes) and respond in a consistent density-dependent manner to changes in habitat quality and quantity in gradually fluctuating systems, such as floodplain pools. Thus, indices of biotic integrity must consider the suite of life history strategies present in the species assemblage to infer the characteristics of a normal or unperturbed system. Ordination of species according to life history strategies could significantly improve predictions about community structure, response to disturbances, and enhance IBIs.

Additional considerations

Life history theory could be used to address a host of management issues in addition to those discussed above. For example, how do we predict effects of invasive species? Most exotic introductions do not become established, so are there common characteristics among species that become established? Kolar and Lodge (2002) examined several life history and ecological attributes of fishes introduced into the Great Lakes of North America. Species that became established had faster growth and tolerated a wide range of temperatures and salinity, but species that spread quickly after establishment had slower growth and tolerated even wider temperature ranges but were intolerant of high water temperatures. Nuisance species have smaller eggs, wider salinity tolerance, and tolerated low temperatures. Their statistical model predicted the sequence of establishment, spread, and impact with >80% accuracy, and it would be interesting to examine life history as correlated suites of attributes (i.e., strategies or syndromes).

Another current issue in fisheries management is the function of artificial reefs and marine reserves. Does the creation of more habitat translate into more fish? According to Grossman et al. (1997), "it appears that both recruitment and post-recruitment processes may limit adult population size of coral reef fishes. The relative importance of the two types of processes depends on the species being examined." A major goal of marine reserves is to protect a sufficient biomass of adults to replenish regional stocks. In this context, Roberts (1997) noted that fish assemblages contain a diversity of life histories (see also Winemiller 1989; Whitfield 1990), so

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that reserves might be one of the only viable means of affording protection for stocks supporting multispecies fisheries.

A major challenge for management of multispecies fisheries is to predict the consequences of altered food web structure for community and production dynamics. As large, long-lived species are depleted, they tend to be replaced in the fishery by species with more rapid life cycles and greater demographic resilience (Jennings et al. 1999*b*; Rochet 2000; Denney et al. 2002), a sequence commonly referred to as the fishing down phenomenon. Community-level density compensation is evident in the fishing down phenomenon (Pauly et al. 2000). For example, catch data from longline fisheries in the Indo–Pacific region reveal a rapid 80% reduction in stocks of marlin in Pacific waters followed by a compensatory increase in faster growing, earlier maturing species, such as sailfish (Myers and Worm 2003). In relatively simple predator–prey systems, harvest of adult piscivores can lead to depensation in the piscivore population via compensatory cultivation of prey that compete with juvenile life stages (Walters and Kitchell 2001). Two-species models with size-dependent functional response and competition between adult prey and juveniles of the piscivore population can yield complex dynamics (De Roos and Persson 2002). Food web models that simulate density-dependent foraging dynamics and allow species to vary in their life history attributes (e.g., differential allocation of assimilated energy into growth, reproduction, foraging) can yield nonlinear responses that may hinder efforts to find simple correlations between predator and prey populations in time-series data (Walters et al. 2000; Matsuda and Abrams 2004; Abrams and Matsuda 2005).

Fisheries bycatch (estimated at over 27 million tons per year) has the potential to impact nontarget species with unknown consequences for food web dynamics affecting target species (Crowder and Murawski 1998). To argue that bycatch causes no harm to nontarget stocks implicitly assumes significant density compensation and the absence of food web and ecosystem consequences. To argue that bycatch harms nontarget stocks assumes that density-dependence is insignificant or too weak to keep pace with bycatch mortality or that compensatory responses may be impeded by ecosystem impacts affecting resource dynamics (e.g., benthic production disrupted by bottom trawling). Conservation and restoration of stocks affected by multispecies fisheries will be enhanced by examining the manner in which species life history strategies yield density compensation and population resilience (e.g., Schindler et al. 2002).

When we consider the potential for abiotic environmental drivers (affecting recruitment dynamics, migration, and habitat productivity) and life history strategies (slow versus fast life cycles, degree of compensatory density dependence) to influence food web dynamics, the challenge of making predictions seems daunting. Even the most precautionary approaches are risky if we fail to understand the basic mechanisms driving population and community dynamics and the scales on which they operate. In most circumstances, adaptive management (field experiments) and simulation modeling probably will yield more useful guidance than simple management targets based on assumptions of S–R models, such as maximum sustainable yield or biological reference points. In the absence of guidance from experiments and detailed simulation models, life history theory and species ordination provide a qualitative basis for managing in the face of inherent uncertainty. For example, Pope et al. (2000) used two life history parameters (K from the von Bertalanffy growth equation and natural mortality at length, M, estimated from body weight) to estimate population vulnerability to fishing mortality for two species in the North Sea. Beverton (1998) proposed that such efforts, expanded to the full range of life history strategies, could provide guidance for fisheries management when empirical data are lacking and model predictions are uncertain.

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Lack of relationship between simulated fish population responses and their life history traits: inadequate models, incorrect analysis, or site-specific factors?[1]

Kenneth A. Rose

Abstract: Relationships between fish population responses to changes in their vital rates and commonly available life history traits would be a powerful screening tool to guide management about species vulnerability, to focus future data collection on species and life stages of concern, and to aid in designing effective habitat enhancements. As an extension of previous analyses by others, I analyzed the responses to changes in fecundity and yearling survival of age-structured matrix and individual-based population models of 17 populations comprising 10 species. Simulations of the matrix models showed that the magnitude of population responses, but not the relative order of species sensitivity, depended on the state (sustainable or undergoing excessive removals) of the population. Matrix and individual-based models predicted population responses that appeared to be unrelated to their species-level life history traits when responses were plotted on a three-end-point life history surface. Density-dependent adult growth was added to the lake trout (*Salvelinus namaycush*) matrix model, and simulations demonstrated the potential importance to predicted responses of density-dependent processes outside the usual spawner–recruit relationship. Four reasons for the lack of relationship between population responses and life history traits related to inadequate population models, incorrect analysis, inappropriate life history model, and important site-specific factors are discussed.

Résumé : Les relations entre les réactions des populations de poissons aux changements de leurs taux vitaux et les caractéristiques démographiques communément disponibles pourraient être des outils puissants de dépistage pour renseigner les gestionnaires sur la vulnérabilité des espèces, pour mieux cibler les récoltes futures de données sur les espèces et les stades de développement qui sont des sujets de préoccupation et, enfin, pour aider à mettre au point des améliorations efficaces des habitats. En continuité avec des analyses antérieures par d'autres chercheurs, mon analyse porte sur les réactions aux changements de fécondité et de survie des animaux de 1 an de modèles démographiques matriciels structurés d'après l'âge et de modèles centrés sur l'individu de 17 populations comprenant 10 espèces. Les simulations des modèles matriciels montrent que l'importance des réactions de la population, mais non l'ordre relatif de sensibilité des espèces, dépendent de l'état (récolte soutenable ou retraits excessifs) de la population. Les modèles matriciels et ceux centrés sur l'individu prédisent des réactions des populations qui semblent indépendantes de leurs caractéristiques démographiques spécifiques, lorsque les réactions sont portées sur un graphique démographique comportant trois points extrêmes. Si on ajoute une croissance adulte reliée à la densité au modèle matriciel du touladi (*Salvelinus namaycush*), les simulations montrent l'importance potentielle pour les réactions prédites de processus reliés à la densité distincts des relations habituelles entre les reproducteurs et les recrues. La discussion porte sur quatre raisons qui expliquent le manque de relation entre les réactions des populations et leurs caractéristiques démographiques, soit des modèles de population inadéquats, une analyse fautive, des modèles démographiques non appropriés et des facteurs importants spécifiques aux sites.

[Traduit par la Rédaction]

Introduction

Understanding and forecasting how fish populations will respond to changes in their vital rates (reproduction, mortality, growth) has been the focus of research and speculation for decades. Marine fisheries management in the United States is governed by the Sustainable Fisheries Act, whose implementation includes estimation of the current status of the fish

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K.A. Rose. Coastal Fisheries Institute and Department of Oceanography and Coastal Sciences, Energy, Coast, and Environment Building, Louisiana State University, Baton Rouge, LA 70816, USA (e-mail: karose@lsu.edu).

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stock, forecasts of annual yields under different harvesting scenarios, and if needed, specification of recovery plans for overfished stocks (Restrepo et al. 1998). Forecasting population trajectories and estimating sustainable harvests have focused fisheries management on stock-assessment methods based on surplus-production models, age-structured statistical models (e.g., virtual population analysis and catch-at-age), and age-structured matrix projection models (Quinn and Deriso 1999). For populations with sufficient site-specific data, this quantitative population-oriented approach is reasonable, although ecosystem-level considerations are receiving increasing attention (Alaska Sea Grant 1999; National Marine Fisheries Service 1999).

Often, even when data are sufficient for development of a site-specific model, certain model parameters are estimated from information on other populations or species. For example, Rose and Cowan (2003) used red grouper (*Epinephelus morio*) in the Gulf of Mexico to illustrate how models and data can affect management decisions. One of the most critical parameters of the age-structured matrix projection model used for determining stock status and forecasting yields into the future was the steepness of the spawner–recruit relationship. Steepness is a measure of how quickly the predicted number of recruits approaches the maximum recruitment level with increasing spawning stock, and is defined as the fraction of maximum recruitment expected when the spawning stock is at 20% of its virgin (no fishing mortality) level (Haddon 2001). Because there were no spawner–recruit data for red grouper, several values of the steepness parameter were used, based on values from similar species that had spawner–recruit data. Life history theory was used to assign species to one of three end-point strategies (Rose et al. 2001), and steepness values from the strategy most similar to red grouper were used in the analysis.

The need for simple rules that use readily available life history traits to infer parameter values or population sensitivity to harvesting is even more important for the many species for which data are simply too sparse to support formal population modeling. The National Marine Fisheries Service (2003) reported that in 2002 the status of fish stocks in the US Exclusive Economic Zone with respect to overfished was unknown for 99 of 259 major stocks (> 90 909 kg landed) and for 596 of 673 minor stocks (< 90 909 kg landed). Meta-analysis offers a promising approach for estimating parameter values from other populations and species (e.g., Myers 2001). Some simple rules for inferring which of the data-poor species might be most vulnerable to harvesting would provide a systematic method for prioritizing already-stretched fisheries-management people and monetary resources.

Data limitations can also arise when the investigation changes from determining the effects of harvesting to other issues such as the effects of changes in habitat. The inclusion of habitat issues in the Sustainable Fisheries Act, and general concerns about accelerating habitat losses, have led to increased interest in habitat effects on fish (Benaka 1999). Recently, US Environmental Protection Agency rules regarding the permitting of power-plant withdrawals of water for cooling include an option that the permittee can use enhancements (e.g., add habitat, stocking) to offset power-plant-induced mortality (Anonymous 2002). Without extensive site-specific data and detailed models, quantifying the effects of various changes in habitat on fish populations is very difficult (Rose 2000). Yet in a given situation there are many options for habitat enhancements, and information on the species and life stages most likely to respond would be useful.

There is clearly a great need for general rules about how species respond to changes in their vital rates, and about the relative sensitivity among life stages to these changes. Life history traits are available or estimable for many species. If rules could be developed that use these readily available life history traits, a potentially powerful management and screening tool could be formulated. Such a tool could be used in data-poor situations to guide management about species vulnerability, to focus future data collection on species and life stages of concern, and to aid in designing the effective habitat enhancements.

In this paper I use a suite of population-dynamics models of a variety of populations and species to determine if the magnitude of their long-term simulated population responses to changes in fecundity and survival can be related to their life history traits. I first briefly review examples where life history theory has been used to qualitatively and quantitatively relate fish population responses to life history traits. I then present an analysis that used a mix of 17 matrix projection models and individual-based models (IBMs) that simulated long-term fish population dynamics. Fecundity and yearling (age 1 to age 2) survival rates were systematically varied, and percent changes in average population abundance were compared among populations and related back to species-level life history traits. Given that I could not find any obvious patterns in the results, I conclude with a discussion of the possible reasons for this non-result and its broader implications for fisheries management and modeling.

Life history theory and population responses

End-point strategies

The literature is rich with analyses that focus on life history traits and how demographic or physiological constraints limit the combinations of traits that result in viable and persistent populations (Roff 1992; Stearns 1997). Less common are studies that use life history traits to infer how populations should respond to changes in their vital rates. The classic r–K continuum remains an area of active discussion in the literature today (Reznick et al. 2002). Qualitatively, r-selected species are thought to be more resilient to harvesting and quicker to recover than K-selected species (Musick 1999).

Winemiller and Rose (1992) modified the r–K approach to better accommodate the life histories of North American fish species. They analyzed 245 species and proposed a three-end-point continuum (Fig. 1). They concluded that fishes fell on a surface defined by the three extreme strategies denoted equilibrium, periodic, and opportunistic. The equilibrium strategy was similar to K-selected species, and was characterized by delayed maturity, small clutches of large eggs, a high degree of parental care, and intermediate adult survival rates. Opportunistic strategists were characterized by early maturity, many small clutches over a protracted spawning season, and low adult survival rates. Periodic strategists were

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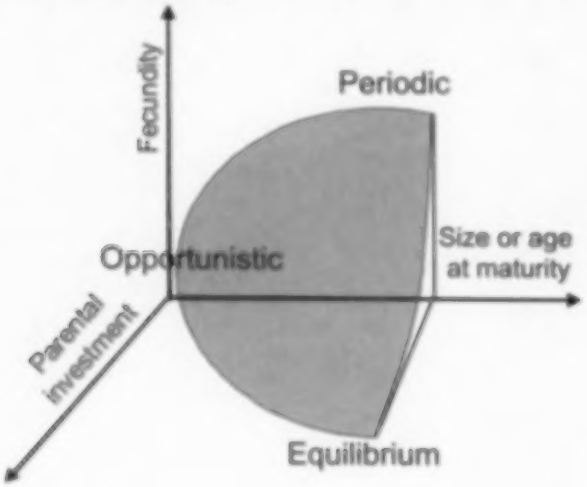
Fig. 1. The three-end-point life history surface for fish proposed by Winemiller and Rose (1992). The end-point strategies are labeled equilibrium, opportunistic, and periodic.



characterized by delayed maturity, large clutches, and high adult survival rates. Species that are representative examples are smallmouth bass (*Micropterus dolomieu*) for the equilibrium strategy, bay anchovy (*Anchoa mitchilli*) for the opportunistic strategy, and striped bass (*Morone saxatilis*) for the periodic strategy. Winemiller (2005) discusses the implications of the three end-point strategies for sustainable harvest, endangered species, stocking, population health indicators, and multispecies interactions.

Several subsequent analyses generally supported the three end-point strategies proposed by Winemiller and Rose (1992). Vila-Gispert and Moreno-Amich (2002) performed a very similar analysis to that of Winemiller and Rose (1992) on 25 freshwater fish species from European waters. Their analysis was in general agreement with that of Winemiller and Rose (1992), but European fish species showed a more restricted range of strategies. European species included periodic and opportunistic species, but no true equilibrium strategists; those authors also noted that some of their periodic strategists were intermediate between periodic and equilibrium strategists. McCann and Shuter (1997) looked at the allometry of reproduction within the context of the three end-point strategies of Winemiller and Rose (1992). They found that the three end-point strategies did provide constraints that were consistent with empirical relationships between ovary weight and body weight and between age at maturity and weight at maturity. They also concluded that salmonids are likely best considered a fourth strategy. Spencer and Collie (1997) analyzed time-series data of catch-per-unit-effort or catch of 30 stocks and related their six groupings of population fluctuations to the three end-point life history strategies of Kawasaki (1983), which directly map to the three end-point strategies of Winemiller and Rose (1992).

Using a different statistical approach than that used by Winemiller and Rose (1992), Rochet et al. (2000) analyzed the interpopulation and interspecific variation of seven traits among 84 populations of 49 species. They applied an autoregressive model to a suite of traits such as time to 5% survival and body length at sexual maturity. The autoregressive model was used to explain variation in each of the traits across populations within species (intraspecific) and among species (interspecific). Each population also had an associated fishing-mortality rate. Principal components analysis was then applied to the "corrected" values of the traits (predicted from the autoregressive models) to identify groupings, and mean values of corrected traits were computed for each of three groupings of fishing-mortality rates. Rochet et al. (2000) interpreted the results of the principal components analysis as two axes: one was a slow-turnover to fast-turnover continuum and the second was the schedule of how energy is allocated to growth versus reproduction. They related their axes to the three end-point strategies of Winemiller and Rose (1992) and concluded that periodic species should have the highest resilience to fishing.

Predicted responses to mortality

Rose et al. (2001) ventured further with the Winemiller and Rose (1992) framework and suggested how the three different end-point strategies would respond to changes in mortality rates. Rose et al. (2001) distinguished between compensation and compensatory reserve. Compensation is the net effect of the density-dependent processes that cause negative feedback on population size. Compensatory reserve is "excessive reproductive capacity under ideal conditions for individual reproduction (Christensen and Goodyear 1988)". Stronger compensation implies less variation in population size over time, while higher compensatory reserve implies greater resilience to increases in mortality. Rose et al. (2001) hypothesized that periodic strategists should show the weakest compensation (high population variation) but the highest compensatory reserve, while equilibrium strategists should show the strongest compensation but the lowest compensatory reserve. They evaluated this hypothesis by comparing estimates of steepness and residual variation of spawner–recruit relationships of 249 populations (57 species) from the Myers spawner–recruit database (Myers et al. 1995). Steepness is the fraction of maximum recruitment at 20% virgin (unfished) stock biomass, and is a measure of compensatory reserve. Residual variation (defined below as the standard deviation (σ) of the spawner–recruit fits to data) was interpreted as an indicator of compensation. Plotting the steepness and residual-variation values with species grouped into Winemiller and Rose's (1992) three end-point strategies, Rose et al. (2001) inferred that the highest steepness values for periodic species and lowest residual-variation values for equilibrium species were consistent with life history theory, and that periodic species should be relatively resilient to fishing. However, there was much variation in steepness and residual-variation values within each life history strategy.

Jennings et al. (1998) included phlyogenetic considerations in their analysis of 18 exploited northeast Atlantic fish stocks (9 species), and showed that the decrease in abundance of stocks that matured later, attained a larger maximum body size, and had lower population growth rates decreased in abundance was greater than would be expected from the fishing-mortality rate. They suggested that some simple life history trait, such as maximum body size, could

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Table 1. The 17 population models involving 10 species used to relate population responses to life history traits.

	Model[a]	Food web[b]	Location
Bay anchovy	I	Population	Chesapeake Bay, mesohaline region
Brook trout	I	2-species competition	Appalachian stream, third order
Lake trout	M	Population	Lake Opeongo; after cisco introduction
Menhaden	M	Population	Mid-Atlantic Bight
Northern anchovy	M	Population	Central California
American shad	M	Population	Connecticut River
Smallmouth bass	M	Population	Lake Opeongo
Striped bass	M	Population	US east coast
	I	Population	San Francisco estuary
Winter flounder	M	Population	Niantic River
	I	Population	Niantic River
Yellow perch	I	Population	Lake Mendota
	I	2-species LV	Lake Mendota
	I	2-species HV	Lake Mendota
	I	3-species competition	Lake Mendota
	I	6-species LV	Lake Mendota
	I	6-species HV	Lake Mendota

Note: The six alternative food-web configurations for the yellow perch (*Perca flavescens*) individual-based model are shown in Fig. 2.

[a]M, matrix projection model; I, individual-based model.

[b]LV, low variability; HV, high variability.

be used to indicate the vulnerability of a population to fishing.

Quantitative evaluations with population models

There have been several analyses that have used population models to quantitatively evaluate the predictions of life history theory for fish. These approaches have generally used age-structured matrix projection models to examine how population responses to changes in mortality rate can be related to life history traits.

Fromentin and Fonteneau (2001) used principal components analysis to analyze the life history traits of 10 tuna and tuna-like species, and determined that the tropical species were characterized by a shorter life-span, smaller body size, longer spawning season, more rapid growth, and younger age at maturity than temperate-zone species. They then developed age-structured models with a spawner–recruit relationship for eggs to young-of-the-year juveniles for species with two contrasting life histories: tropical skipjack tuna (*Katsuwonus pelamis*) and temperate-zone Atlantic bluefin tuna (*Thunnus thynnus*). The models were modified to accommodate monthly spawning over the entire year for the tropical skipjack tuna. Several scenarios of fishing-mortality rates were simulated for 200 years. They concluded that the tropical skipjack tuna (*r*-selected traits) was resistant to fishing, whereas the temperate-zone Atlantic bluefin tuna (*K*-selected traits) was vulnerable to collapse if harvest was imposed prior to their age at maturation.

Rochet (2000) used deterministic, density-independent stage-based matrix models to compare life history traits during high and low population abundance periods for Greenland halibut (*Reinhardtius hippoglossoides*) and plaice (*Pleuronectes platessa*). She computed the sensitivity of the finite population growth rate (λ) and, by comparing high- and low-abundance periods between the species, concluded that changes in life history traits towards a younger age at maturity, decreased proportion of repeat spawners, and increased fecundity at age could be used to infer the effects of fishing and population viability.

Schaaf et al. (1987, 1993) used age-structured matrix projection models of 12 populations (8 species and one population divided into three time periods) to relate predicted population responses to life history traits. They used density-independent, deterministic age-structured matrix models, solving for the survival rate in the first year that would stabilize each population trajectory. They decreased either first-year or age-1 and older survival rates for 1 year only or permanently, and computed various metrics of population responses. The population response to one-time reductions in survival was the number of years required for the population to stabilize, which was positively related to a heuristic index of reproduction based on age-specific survival rates and fecundity. Stabilization was longer for those species that delayed reproduction and quickest for those species whose reproduction was well dispersed among ages. Responses to permanent changes in first-year or age-1 and older survival rates were compared among populations by computing the finite population growth rate (λ) for a series of reductions in survival rates. Schaaf et al. (1993) summarized each population's response as the slope of the regression of changes in $\ln(\lambda)$ versus percent changes in survival rates. They then related the slopes to differences in the life history traits and habitat-usage patterns of the populations.

Barnthouse et al. (1990) used age-structured matrix projection models to compare the responses of Gulf menhaden (*Brevoortia patronus*) and striped bass to increased mortality. Their matrix projection models included both density-dependence (Ricker spawner–recruit relationship) and interannual stochasticity in young-of-the-year survival. They used laboratory toxicity data as the basis for reducing young-of-the-year survival, and performed one hundred 100-year simulations for baseline (no contaminant) and three lev-

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els of increased mortality. They inferred the importance of life history by noting that Gulf menhaden (small bodied, short-lived) had greater tolerance to increases in young-of-the-year mortality than striped bass (large bodied, long-lived).

Segue to my analyses

My analyses in this paper can be viewed as an extension of these previous analyses. I used models that included both density-dependence and stochasticity, and I simulated a wide variety of species. The previous analyses were heading in the right direction in terms of quantitative evaluation of life history theory predictions, but used either density-independent or deterministic matrix models (Schraaf et al. 1993; Rochet 2000) or included density-dependence but simulated only a few species (Barnthouse et al. 1990; Fromentin and Fonteneau 2001). I also attempt to place my results in the context of the Winemiller and Rose (1992) framework of three end-point life strategies, which appears to be a robust representation of life history strategies of fish.

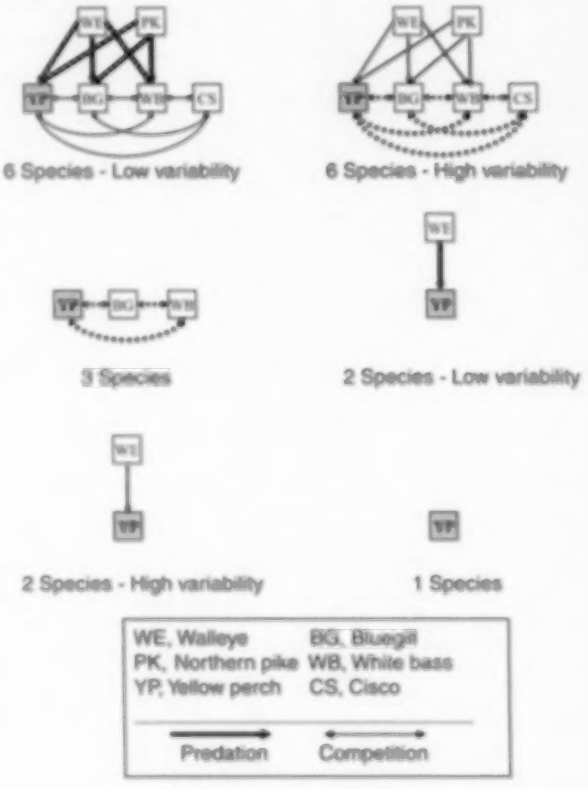
Methods: population models and simulations

I used models of 17 populations comprising 10 different species (Table 1). These models were of two types: age-structured matrix projection and individual-based. I had matrix models and IBMs of the same population (Niantic River winter flounder, *Pleuronectes americanus*) and for two different populations of the same species (Chesapeake Bay and San Francisco Estuary striped bass). For yellow perch (*Perca flavescens*), the IBM was configured for the environment of Lake Mendota, with yellow perch imbedded into six different food webs (Fig. 2). The remainder of the matrix projection models and IBMs were of different species. The species simulated with matrix models were selected on the basis of the availability of spawner–recruit data and well-documented survival, maturation, and fecundity rates by age. IBMs are much more difficult to use than matrix models because each involves a customized computer code. The species simulated with IBMs involved my participation and I had first-hand knowledge of the history of model development and the computer code. When put together, the species analyzed had a wide variety of life history strategies and traits.

Matrix projection models

The matrix projection models were formulated similarly among species. The species were selected to ensure a range of life history strategies, and because these particular populations had long time series of (what I judged to be high-quality) spawner–recruit data. The models followed the total numbers of male and females (females only for winter flounder) on an annual basis; age-specific survival, maturity, and fecundity (eggs per mature female) rates were obtained from literature reviews (Public Service Electric and Gas Company 1999) and from data provided by investigators familiar with the populations (Tables 2 and 3). First-year survival was represented as a Beverton–Holt spawner–recruit function fitted to the data (Fig. 3). Both Beverton–Holt and Ricker functions were fit using nonlinear regression, and in all cases the Beverton–Holt function provided a similar or better fit.

Fig. 2. Six alternative food webs for the yellow perch (*Perca flavescens*) individual-based model. All versions used the same environmental conditions representative of Lake Mendota. Arrows denote whether the dynamics were dominated by competition for common prey resources among the planktivores (high variability) or by piscivore predation on the planktivores (low variability).



Based on the Beverton–Holt fit, the mean ($\bar{x}$) and standard deviation (σ) of the natural-log-transformed residuals (log predicted – log observed) were computed and used as parameters of a lognormal distribution (Cordue 2001). For each year of the simulation, a random deviate was generated from the lognormal distribution (exponentiation of normal distribution with $\bar{x}$ and σ), and used to multiply the recruitment for that year. All matrix-model simulations except lake trout (*Salvelinus namaycush*) were for 200 years, with average values of total population number computed for years 51–200. Lake trout simulations were for 500 years, with means computed for years 201–500, to allow the simulated population to completely respond to changes in fecundity and yearling survival rates.

For striped bass and northern anchovy (*Engraulis mordax*), the weight of spawners in the spawner–recruit relationship was reported in metric tons. I determined a multiplier for each of these species that converted total eggs computed in the model to metric tons for use in the spawner–recruit relationship. Using trial and error simulation, I found multipliers of total eggs of 3×10^{-10} for northern anchovy and 5×10^{-9} for striped bass that resulted in

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Table 2. Age-specific mortality (fraction per year), fraction mature times fecundity per mature female (eggs·female^{-1}), and weight per individual (grams wet weight) for the American shad (*Alosa sapidissima*; SH), Atlantic menhaden (*Brevoortia tyrannus*; ME), and northern anchovy (*Engraulis mordax*; NA) matrix population models.

Age	Annual mortality			Maturity × fecundity (× 10^6)			Weight per individual		
	SH	ME	NA	SH	ME	NA	SH	ME	NA
1	0.32	0.81	0.75	0.00	0.63	2.02	140.0	114.6	8.7
2	0.32	0.79	0.75	0.00	7.34	9.35	530.0	266.1	14.6
3	0.32	0.79	0.75	0.00	18.44	19.45	1050.0	427.5	18.3
4	0.49	0.79	0.75	5.75	29.13	27.99	1590.0	566.7	21.2
5	0.76	0.79	0.75	2.15	39.29	32.75	2070.0	674.2	24.5
6	0.85	0.79	0.75	41.53	47.78	32.75	2480.0	752.1	24.3
7	0.85	0.79	0.75	45.97	54.31	32.75	2810.0	806.6	24.5
8	0.85	0.79		49.36	59.06		3070.0	843.7	

Note: Mortality is defined as the fraction dying from age i to age $i + 1$; survival from egg to age 1 was determined by a spawner–recruit relationship. A female to male sex ratio of 1:1 is assumed for all species. Data for American shad and Atlantic menhaden are from Public Service Electric and Gas Company (1999) and for northern anchovy from Butler et al. (1993).

Table 3. Age-specific mortality (fraction per year), fraction mature times fecundity per mature female (eggs per mature female), and weight per individual (grams wet weight) for the lake trout (*Salvelinus namaycush*; LT), smallmouth bass (*Micropterus dolomieu*; SM), striped bass (*Morone saxatilis*; SB), and winter flounder (*Pleuronectes americanus*; WF) matrix population models.

Age	Annual mortality				Maturity × fecundity				Weight per individual			
	LT	SM	SB	WF	LT	SM	SB	WF	LT	SM	SB	WF
1	0.12	0.26	0.67	0.4	0	0	0	0	3.81	5.2	175	4.98
2	0.12	0.26	0.25	0.3	0	0	0	0	29.9	30.1	620	56.7
3	0.12	0.48	0.20	0.3	0	0	0	0.3	94.4	83.8	1388	251.3
4	0.12	0.30	0.30	0.5	0	0.1	0.1	1.3	205.2	178.3	2427	367.9
5	0.12	0.40	0.36	0.5	0	0.5	0.8	5.2	364.1	276.4	3658	494.0
6	0.35	0.51	0.37	0.5	0	1.0	4.3	7.8	368.7	469.9	5000	624.6
7	0.35	0.57	0.37	0.5	0	1.5	11.9	10.0	813.8	627.5	6384	746.2
8	0.35	0.62	0.37	0.5	0	2.0	16.2	12.0	1093.0	781.6	7756	849.6
9	0.35	0.58	0.37	0.5	0.1	2.4	21.1	13.6	1399.7	937.0	9078	933.1
10	0.35	0.58	0.37	0.5	0.20	3.0	24.9	15.0	1726.5	1157.6	10322	999.3
11	0.35	0.60	0.37	0.5	0.30	3.3	28.6	15.9	2067.0	1307.2	11474	1045.1
12	0.35	0.64	0.37	0.5	0.36	3.53	32.0	16.8	2415.0	1358.9	12526	1084.1
13	0.35	0.62	0.37	0.5	0.41	3.53	35.2	17.5	2766.5	1360.8	13478	1116.3
14	0.35		0.37	0.5	0.46		38.1	18.0	3115.9		14328	1141.3
15	0.35		0.37	0.5	0.52		40.7	18.5	3460.0		15084	1157.6
16	0.35		0.37		0.57		430.8		3795.7		15752	
17	0.35		0.37		0.62		451.6		4120.9		16339	

Note: For comparison with other species, the fecundity values for winter flounder used in this table are double those used in the matrix-model simulations (i.e., convert female eggs per mature female to eggs per mature female). The fraction mature × fecundity is × 10^6 for lake trout and smallmouth bass and × 10^5 for striped bass and winter flounder. Mortality is defined as the fraction dying from age i to age $i + 1$; survival from egg to age 1 was determined by a spawner–recruit relationship. A female to male sex ratio of 1:1 is assumed for all species. Data for lake trout and smallmouth bass were provided by B. Shuter, Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada, personal communication; data for striped bass are from Public Service Electric and Gas Company (1999), and for winter flounder from Northeast Utilities Environmental Laboratory (2002).

recruitment values that were in the middle of the range of their observed recruitment levels.

Standardization of matrix models

I standardized the population state simulated by the matrix models across the seven populations. Predicted responses to changes in fecundity and survival rates could depend on the state of the population, which would confound comparisons among species. Depressed populations would likely show greater responses than populations near their carrying capacity. I therefore assessed the effects of population state on predicted population responses. I did not adjust the spawner–recruit relationships because they were site-specific. Rather, I achieved a variety of population states for each matrix model by adjusting the annual survival fractions of the age-1 and older age classes. Natural and fishing survival rates were less site-specific than the spawner–recruit relationships. Changing adult mortality is a

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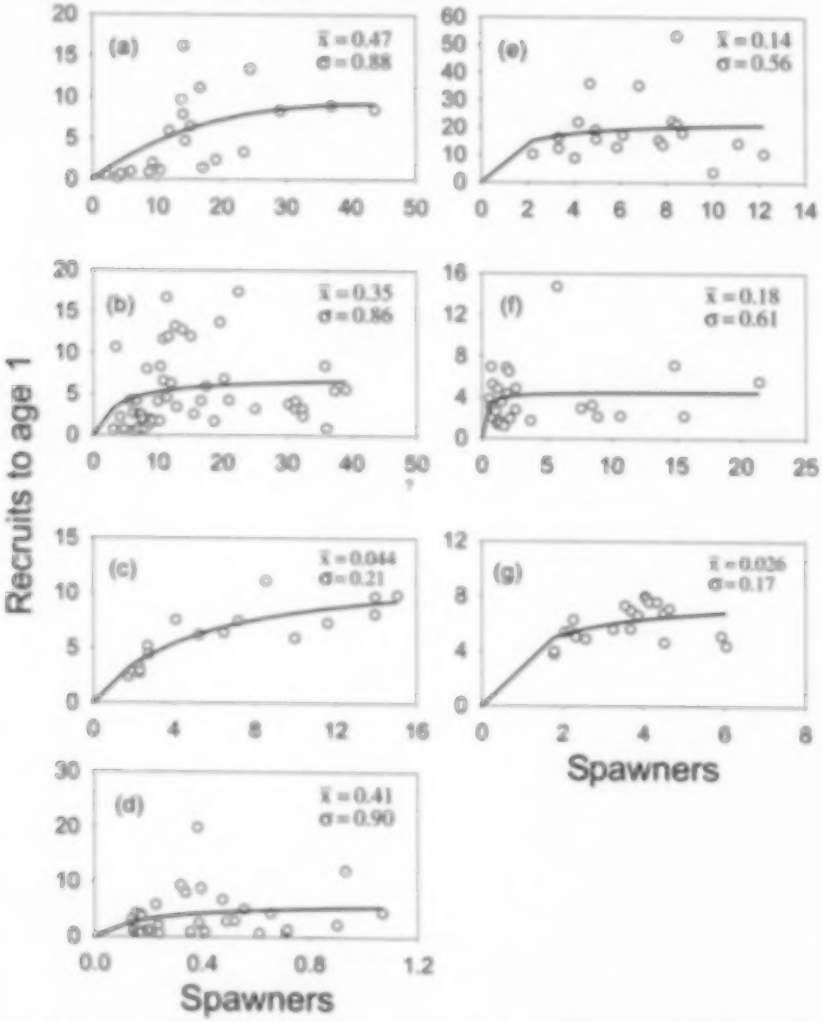
Fig. 3. Spawner–recruit data and fitted Beverton–Holt relationships used in the matrix models. The mean ($\bar{x}$) and standard deviation (σ) of the log-transformed residuals used to generate lognormal variability in recruitment are shown. (*a*) Winter flounder, *Pleuronectes americanus* (10^9 female eggs and 2×10^4 female recruits). (*b*) Smallmouth bass, *Micropterus dolomieu* (10^6 eggs and 10^3 recruits). (*c*) Striped bass, *Morone saxatilis* (10^3 tonnes (t) and 10^6 recruits). (*d*) Northern anchovy, *Engraulis mordax* (10^5 t and 10^7 recruits). (*e*) American shad, *Alosa sapidissima* (10^{10} eggs and 10^6 recruits). (*f*) Atlantic menhaden, *Brevoortia tyrannus* (10^{13} eggs and 10^9 recruits). (*g*) Lake trout, *Salvelinus namaycush* (10^{10} eggs and 10^6 recruits). Sources are as follows: winter flounder, Northeast Utilities Environmental Laboratory (2002), data for age-1 recruits were approximated from reported fully recruited individuals assuming average survival rates; smallmouth bass, B. Shuter, Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, personal communication; striped bass, Myers et al. (1995); northern anchovy, Pacific Fishery Management Council (1998), recruits were converted from biomass on 1 July to numbers on the following 15 February (about 1 year old) assuming an individual weighed 8.7 g and the survival rate was 40% (Butler et al. 1993); American shad, Savoy and Crecco (1988); Atlantic menhaden, Vaughan and Smith (1988), Vaughan (1990); lake trout, B. Shuter (personal communication).



reasonable way to put the populations in depressed versus sustainable states.

I standardized the matrix models using an approach analogous to that used in marine fisheries management in the United States (Rose and Cowan 2003). US fisheries management uses the metrics of long-term average yield and the spawning stock associated with this yield. Because I specified total mortality rates for adults, I computed the sustainable total removal (analogous to yield from fishing) as the annual biomass (number by age times mean weight by age) generated from mortality of age-1 and older age classes. The spawning stock associated with each level of sustainable removal was computed as the average annual total number of eggs produced. I ran series of simulations for each population in which I incrementally increased or decreased age-1 and older survival by a multiplier (e.g., 0.9, 1.0, 1.1). This resulted in a plot of sustainable removals on the y axis versus the associated changes (multiplier value) in adult sur-

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Table 4. Characteristics of the five individual-based models used in the analysis: bay anchovy, *Anchoa mitchilli* (BA), brook trout, *Salvelinus fontinalis* (BT), striped bass (SB), winter flounder (WF), and yellow perch (YP).

Model	Time step	Spatial grain	Currency	Source
BA	Daily	Single box	Individuals	Rose et al. 1999
BT	Daily	Series of 45 hydrologically linked pool, run, and riffle habitat cells	Individuals	Clark and Rose 1997*a*, 1997*b*, 1997*c*
SB	Daily for YOY; annual for age 1 and older	Four connected boxes representing upper Sacramento, lower Sacramento, San Joaquin, and Suisin areas	Individual for YOY; age classes for age 1 and older	K.A. Rose, J.H. Cowan, L.W. Miller, D.E. Stevens, W.J. Kimmerer, and R.L. Brown, unpublished data
WF	Daily for YOY; annual for age 1 and older	Single box	Individuals for YOY; age classes for age 1 and older	Rose et al. 1996
YP	Daily	Connected epiliminion, hypolimnion, and littoral habitat boxes	Individuals	McDermot 1998; McDermot and Rose 2000

Note: YOY, young-of-the-year.

vival on the *x* axis. In all cases, these plots were dome-shaped, although some populations generated relatively flat curves. The dome shape implies that some intermediate level of adult survival generated the maximum removable biomass, which is analogous to the commonly assumed dome-shaped relationship between yield and fishing-mortality rate. I determined the multiplier of adult survival that resulted in the maximum sustainable removal (MSR), which was the peak of the dome-shaped relationship, and the spawning stock (total eggs) associated with that level of MSR (denoted SS_{MSR}). For each population I then determined the multiplier needed to achieve a spawning stock at 25% SS_{MSR} (sustainable), 10% SS_{MSR} (heavy removal), and 5% SS_{MSR} (over-removal). I also included the initial set of adult survival rates estimated from the literature, which I termed arbitrary. All simulations involving changes in egg or yearling survival were applied for each of the four versions of each population model (arbitrary and 5%, 10%, and 25% SS_{MSR}).

The designations sustainable, heavy removal, and over-removal were based on population responses to further decreases in adult survival. For most of the matrix models, populations at the 25% SS_{MSR} state, deemed sustainable, were able to withstand further decreases of at least 25%–30% in their adult survival multiplier (i.e., withstand 25%–30% higher annual mortality) with only small decreases in their long-term average abundances. The 10% SS_{MSR} state was labeled heavy removal, based on further decreases of 25% in adult survival, resulting in persistent but noticeably lower population abundances. The 5% SS_{MSR} state was labeled over-removal because further decreases of 25% in adult survival generally caused populations to barely persist or to approach extinction. US fisheries management has used a general guideline that is risk-averse and sustainable to remove 60%–70% of a virgin stock's reproductive potential (Mace and Sissenwine 1993; Myers et al. 1994).

Individual-based models

The IBMs shared several features but, in contrast to the matrix models, differed greatly in their details (Table 4). All of the IBMs simulated growth, mortality, and reproduction for the full life cycle of each population. Models that included multiple spatial boxes also simulated movement of individuals among the boxes. All of the models tracked young-of-the-year individuals on a daily time step, and all represented growth of young-of-the-year life stages with a bioenergetics model. Some of the models tracked individuals throughout their lifetime (yellow perch, brook trout (*Salvelinus fontinalis*), and bay anchovy), while others used simpler age-structured approaches for the adult portion of the life cycle (striped bass and winter flounder). All of the models included potential density-dependent growth in one or more life stages by simulating prey densities through time as the net result of prey production and fish consumption. Depending on the model, density-dependent growth affected survival and reproduction because mortality, maturity, and fecundity rates were size-dependent. Several of the models also included density-dependent mortality (winter flounder, striped bass, and yellow perch). In the spatially explicit models, movement was represented in a variety of ways: inferred from particle-tracking results for eggs and yolk-sac larvae for the San Francisco Estuary striped bass model; based on short-term growth maximization for the trout model; and dependent on water temperature and dissolved oxygen concentrations for the yellow perch model.

In contrast to the matrix models, I did not standardize the population states among the IBMs. The IBMs were developed to be as site-specific as possible. While they used information from other populations and species for model inputs, each of the IBMs was calibrated and evaluated, to varying degrees, against data from the population of interest. In some instances I was wary of running the models under conditions much different than their original site-specific applications without substantial recalibration.

Life history traits

I used the values of life history traits reported by Winemiller and Rose (1992) for the 10 species in this analysis (Table 5). Another option would be to use population-specific values of life history traits consistent with each of the population models. I initially used the general values of the life history traits reported in Winemiller and Rose (1992) in this analysis, as one purpose of the analysis was to see if life history traits could be used to infer population responses in data-poor situations. Subsequent attempts to use life history traits derived from the site-specific models did not significantly alter the results of the analysis. The 10 species

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Table 5. Values of the life history traits for the 10 species for which there were matrix or individual-based population models.

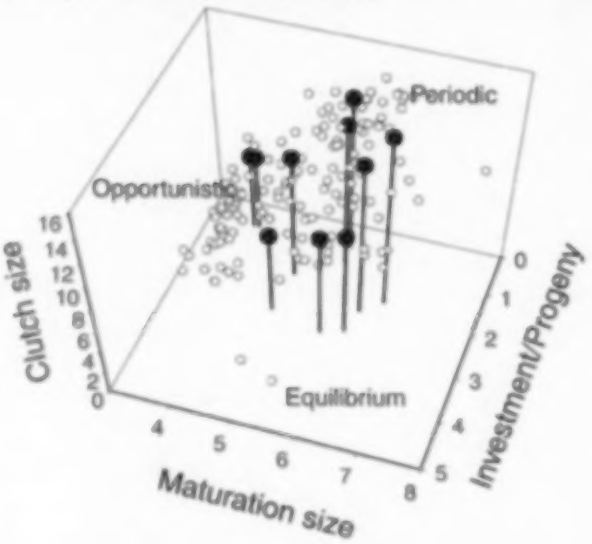
	Maturation length (mm)	Clutch size (eggs·batch^{-1})	Investment per progeny[a]
American shad	461	538 767	2.04
Northern anchovy	99	685	0.59
Lake trout	419	7902	2.56
Striped bass	633	2 462 000	1.72
Smallmouth bass	292	7708	2.71
Winter flounder	250	600 000	0.59
Atlantic menhaden	257	224 134	0.96
Bay anchovy	45	687	0.59
Brook trout	119	1210	2.45
Yellow perch	127	43 680	1.53

Note: The values of the life history traits are the same as those used in analyses reported in Winemiller and Rose (1992).

[a]Computed as log[(parental care + 1) × (egg diameter + 1)], where parental care was coded as 1, 2, 3, or 4 depending on whether eggs were placed in special habitats, whether nests were involved, the duration of parental protection of nest, and the parental contribution to the nutrition of the larvae.

analyzed here cover a reasonable portion of the life history space formed by the 245 species analyzed by Winemiller and Rose (1992) (Fig. 4).

Fig. 4. The positions in life history space of the 10 species used in this analysis (●) compared with those of the 245 species analyzed by Winemiller and Rose (1992) (○).



Design of simulations

I performed three sets of simulations. The first set used the matrix projection models to assess how population state affected population responses. The second set then used the matrix models (under a selected population state) together with the IBMs to predict population responses to changes in fecundity and yearling survival rates, and to relate these responses to life history traits. The third set of simulations used the matrix model of lake trout, without and with adult density-dependent growth rates, to assess how density-dependence in post-young-of-the-year life stages (i.e., outside the spawner–recruit relationship) could influence population responses.

All simulations used ±25% changes in fecundity of all mature age classes and ±25% changes in the yearling (age 1 to age 2) annual survival rate. For the IBMs that represented the yearling life stage on a daily time step, the 25% changes were imposed so that 25% annual changes were achieved (e.g., 25% reduction was a daily multiplier of $\sqrt[365]{0.75} = 0.9992$). Model predictions of population responses are likely sensitive to whether changes are imposed before or after density-dependence operates. My changes to fecundity generally corresponded to a time prior to density-dependence in all of the models. Changes to yearling survival occurred after density-dependence in the matrix models, but were fuzzier in the IBMs. Most of the IBMs included density-dependence during young-of-the-year life stages, but some of the IBMs also predicted significant density-dependent growth and mortality in older life stages.

The first set of simulations imposed the ±25% changes in fecundity or yearling survival in the matrix models for the four different population states. For each, I computed the average total population just prior to reproduction, so that the youngest individuals were just about to turn age 1. The average population was computed for years 51–200 (201–500 for lake trout) for each of the five conditions (baseline, +25% and –25% fecundity, and +25% and –25% yearling survival) at each of the four population states (arbitrary and 5%, 10%, and 25% SSB_{MSR}). I report the population responses as percent change in average population number from the baseline value: % change = $100 \times [(Y - Y_{baseline})/Y_{baseline}]$.

The second set of simulations used both the matrix models and the IBMs to simulate population responses to ±25% changes in fecundity or yearling survival. Because population state did not greatly affect matrix-model predictions of species sensitivity, I used the adult survival rate corresponding to the 5% SS_{MSR} for all of the matrix models. Percent change in the average total population number from baseline was computed and plotted in life history space. The plots used log maturation size, log clutch size, and investment per progeny for the three axes (Table 5); the height of the symbol was that species' position in life history space, and the size (diameter) of the symbol was scaled proportional to the absolute magnitude of its population response. To confirm the interpretation of the three-dimensional surface plots, I also show the responses to the changes in fecundity as a series of three two-dimensional scatter graphs (each graph is a pairwise combination of the three life history traits), with the size of the symbol scaled to the absolute magnitude of the population response.

The third set of simulations added density-dependent adult growth to the matrix model of lake trout to explore the consequences of including density-dependence in the matrix models outside the spawner–recruit relationship. Recent reviews suggest that density-dependent growth in adult fishes may be more widespread than was previously thought (Lorenzen and Enberg 2002). Density-dependent growth has been well documented in adult lake trout (Matuszek et al. 1990; Ferreri and Taylor 1996), and therefore permitted realistic specification in the matrix model. Annual growth in weight increments (grams wet weight per year) were specified as functions of

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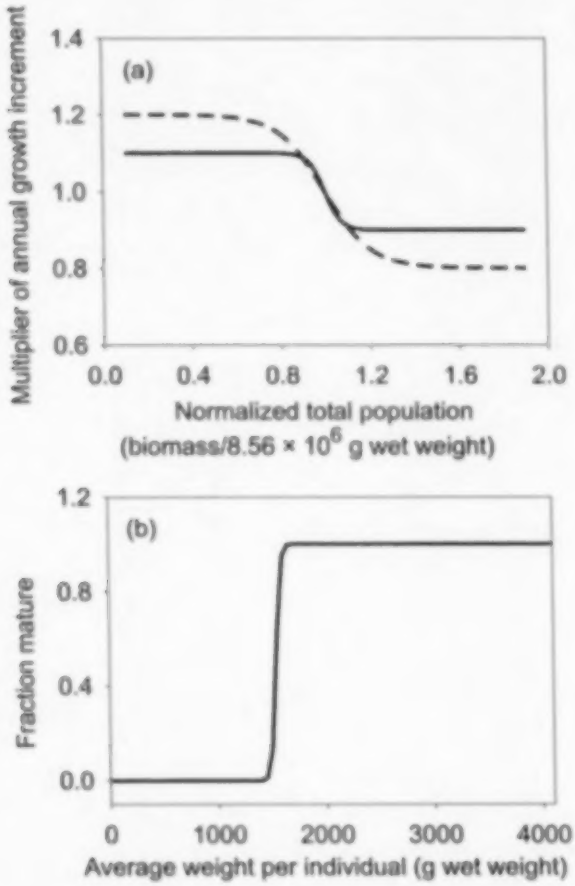

Fig. 5. Density-dependent multiplier of annual growth increments (*a*) and fraction mature as a function of weight (*b*) for the density-dependent adult growth addition to the matrix model of lake trout. In *a*, the solid line represents 10% and the broken line represents 20%.

age from differencing successive weights from the baseline weights at age schedule (shown in Table 3). Two levels of density-dependent adult growth were simulated. I specified two functions (denoted 10% and 20%) that acted as a multiplier of the annual growth increments that were dependent on the total adult (age 1 and older) biomass (Fig. 5*a*). The 10% and 20% density-dependent functions were chosen to very crudely bracket the magnitude of changes in growth rate and age at maturity of adult lake trout observed in Lake Opeongo between the high-abundance period (before the introduction of cisco, *Coregonus artedii*) and the low-abundance period (after the introduction of cisco) (Matuszek et al. 1990). The baseline fecundity and maturity at age values used in the matrix model were converted to functions of body weight using the baseline mean weight at age schedule (fraction mature shown in Fig. 5*b*; fecundity = 0.068958 + 1.506 × body weight in grams). Model simulations were begun with the baseline weight at age values, and each year total population biomass was computed, which determined the density-dependent multiplier of the weight increments. Weight at age was then updated by applying the density-dependent multiplier to the weight increment and adding this to the previous year's weight. Fecundity and fraction mature by age for that year were then determined from the mean weights at age. Simulations of the model under baseline conditions using the dynamic, density-dependent growth were very similar to the simulations that used the fixed fecundity and maturity by age. The ±25% changes in fecundity and yearling survival were repeated using the matrix model that included both the spawner–recruit relationship and density-dependent adult growth, and responses were compared with the matrix model that included the spawner–recruit relationship only.

Replicate simulations

All results shown are based on single matrix-model and IBM simulations. Both types of models involve stochastic simulation using Monte Carlo techniques. While mean total population varied among simulations that used different random-number sequences, percent change from baseline values varied little among replicate simulations. For example, predicted percent responses of the winter flounder matrix model for the 5% SS_{MSR} condition for two different random-number sequences were 20% and 22% for increased fecundity, –36% and –39% for decreased fecundity, 50% and 52% for increase yearling survival, and –52% and –54% for decreased yearling survival. Predicted responses of the IBMs were also robust to whether simulations were run for 50 or 100 years, and among replicate simulations that used different random-number sequences.

Results

Population trajectories

Representative simulations of the population trajectories for the matrix models and IBMs are shown in Fig. 6. Smallmouth bass (Fig. 6*a*) and Atlantic menhaden (*Brevoortia tyrannus*) (Fig. 6*b*) are used to illustrate the interannual variation in total population numbers typical of the baseline matrix-model simulations. Years 20–50 of the yellow perch IBM for the 2-species low-variability food web for the baseline and –25% yearling survival simulations are shown as well (Fig. 6*c*). Also illustrated, using the yellow perch IBM, is the calculation of percent change from baseline for the reduced yearling survival simulation.

Effects of population state

Population state affected the magnitude, but not the general patterns, of population responses among matrix-model species (Fig. 7). For a given species, responses to increased fecundity and decreased fecundity decreased in absolute magnitude with improving population state (the bars get smaller from 5% to 10% to 25% SSB_{MSR} in Fig. 7*a*). However, responses to fecundity across species generally maintained the same rank ordering with improving population state. For each population state, winter flounder and northern anchovy consistently showed the largest responses, while Atlantic menhaden and American shad (*Alosa sapidissima*) consistently showed the smallest responses. The responses to changes in yearling survival (Fig. 7*b*) were generally larger, showed less variation among species, and were relatively less

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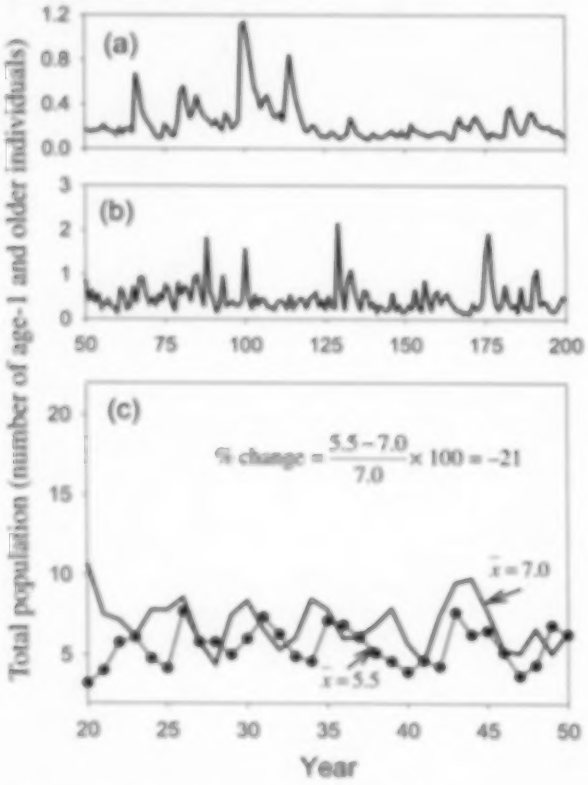
Fig. 6. Time series of total population (number of age-1 and older individuals) for baseline simulations of the smallmouth bass matrix model (10^5 individuals) (*a*), Atlantic menhaden matrix model (10^{10} individuals) (*b*), and yellow perch individual-based model (IBM; 10^5 individuals) (*c*) in the 2-species low-variability food web. Also shown are the total population numbers for the reduced yearling survival simulation of the yellow perch IBM and the calculation of the population response as percent change from baseline. In *c*, the thick line represents baseline values and the thin line with solid circles represents the reduced yearling survival simulation.



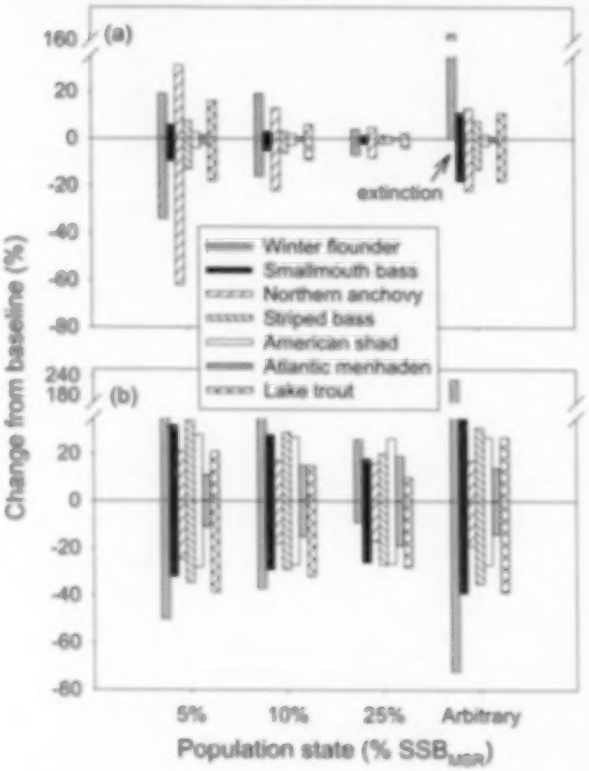
affected by the state of the population than the responses to changes in fecundity. For changes in both fecundity and yearling survival, population responses with the arbitrary values of inputs generally showed the same patterns of species sensitivity as those predicted with the populations in standardized states.

Responses in life history space

The magnitude of responses of the matrix models and IBMs showed no obvious relationship to the three life history traits. Neither large nor small symbols seemed to cluster in particular regions of the life history surface for changes in fecundity (Fig. 8) or for changes in yearling survival (Fig. 9). Pairwise examination of the three life history traits for changes in fecundity also did not show any obvious patterns or clustering in the sizes of symbols (Fig. 10).

The range of responses of yellow perch among its different food webs was, in some cases, comparable to the range of responses across all species. For example, increased fecundity resulted in a range of responses of 1%–31% among all matrix models, 2%–46% for the IBMs other than yellow perch, and 2%–37% among the six alternative yellow perch food webs. These matrix-model predictions were based on the population state of 5% SS_{MSR}, which generally resulted in the largest matrix-model responses. The wide range of predicted responses among the alternative yellow perch food webs was not due to unrealistic food webs. The 2% and 37% responses were obtained from the two 6-species food webs, which were both reflective of the food web in Lake Mendota but were calibrated differently (McDermot and Rose 2000). The yellow perch IBM did not always predict wide-ranging responses. Decreased fecundity resulted in responses of –2% to –62% among the matrix models and –10% to –27% among the IBMs other than yellow perch, compared with a range of only –1% to –6% for yellow perch among all six different food webs.

Fig. 7. Predicted population responses (percent change from baseline) for changes in fecundity (*a*) and yearling survival (*b*) for the matrix models adjusted to 5%, 10%, and 25% SSB_{MSR}, and with the initial arbitrary values of input parameters.



There were no consistent differences in the responses between the matrix models and the IBMs, although such a comparison is weak because of small sample size. Examination of the matrix-model and IBM results separately did not show any obvious clustering of the small or large symbols (open versus shaded circles in Figs. 8 and 9). However, the number of species becomes relatively small when matrix-model and IBM results are viewed separately. Winter flounder responses predicted by the matrix model and IBM were

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Fig. 8. Predicted population responses (percent change from baseline) from the matrix models (shaded circles) and IBMs (open circles) for increased fecundity (*a*) and decreased fecundity (*b*) plotted in Winemiller and Rose (1992) life history space. The height of the symbol is the position of the species on the life history surface, and the size of the symbol is proportional to the absolute magnitude of the predicted response. All responses to increased fecundity were positive (higher average population abundance than baseline), and all responses to decreased fecundity were negative (lower average population abundance than baseline).

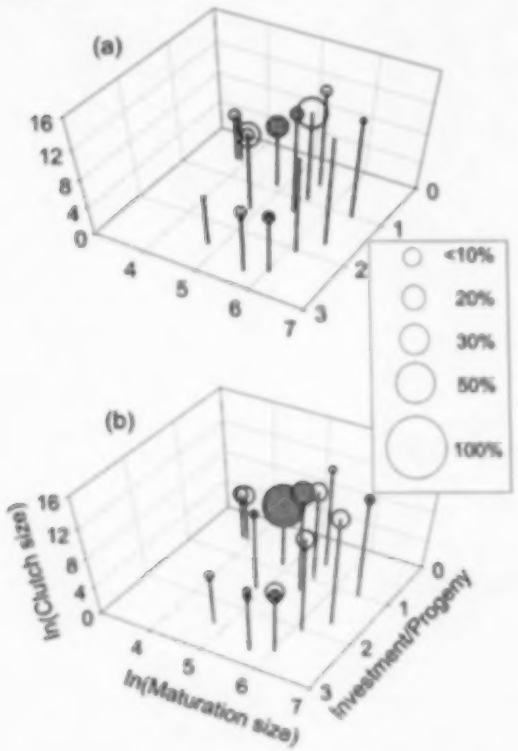
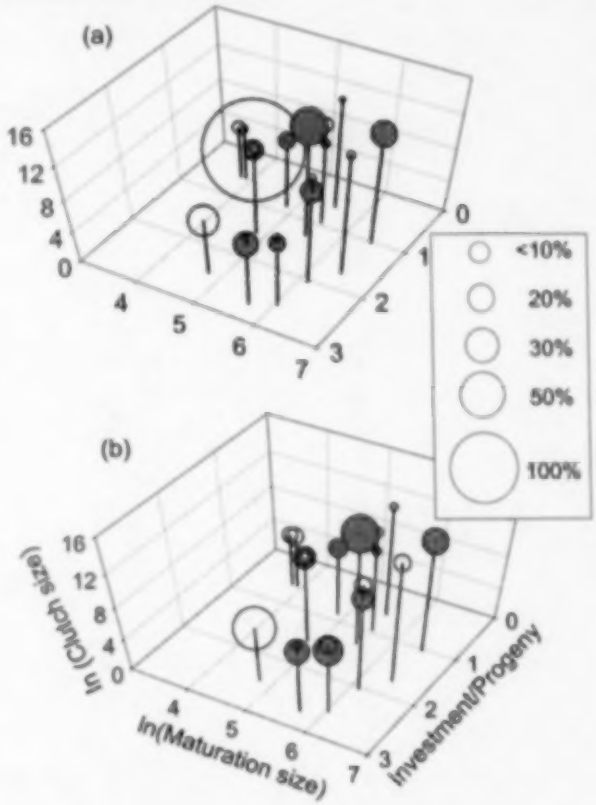


Fig. 9. Predicted population responses (percent change from baseline) from the matrix models (shaded circles) and IBMs (open circles) for increased yearling survival (*a*) and decreased yearling survival (*b*) plotted in Winemiller and Rose (1992) life history space. The height of the symbol is the position of the species on the life history surface and the size of the symbol is proportional to the absolute magnitude of the predicted response. All responses to increased yearling survival were positive (higher average population abundance than baseline) and all responses to decreased yearling survival were negative (lower average population abundance than baseline).



not consistent, even though both models were based on the same Niantic River winter flounder data. Predicted responses for the winter flounder matrix model and IBM were 20% versus 46% for increased fecundity, –36% versus –27% for reduced fecundity, 50% versus 18% for increased yearling survival, and –52% versus –14% for reduced yearling survival.

Effects of adult density-dependent growth on lake trout responses

Realistic levels of density-dependent adult growth dampened population responses of lake trout to changes in fecundity and yearling survival (Fig. 11). The 10% density-dependent function eliminated the lake trout response to increased fecundity and approximately halved the responses to decreased fecundity and to changes in yearling survival. The stronger 20% density-dependent function essentially eliminated (offset) all of the population responses, resulting in population responses of less than 6% for all changes in fecundity and yearling survival.

Discussion

Using life history theory to infer likely fish population responses to changes in vital rates, such as fecundity and survival, has many attractive features. While many species are data-poor, we often know or can estimate their basic life history traits. I would argue that, with some extrapolation and a little effort, we could place many species on the surface shown in Fig. 1. Thus, if population responses to changes in fecundity and survival showed consistent patterns in this life history space, we would have a powerful screening tool for identifying species potentially at risk and the species likely to be most responsive to habitat enhancements. Unfortunately, my analysis did not yield consistent patterns. There are four reasons that could explain my results: inadequate population models, incorrect analysis, inappropriate life history model, or important site-specific factors. I discuss each

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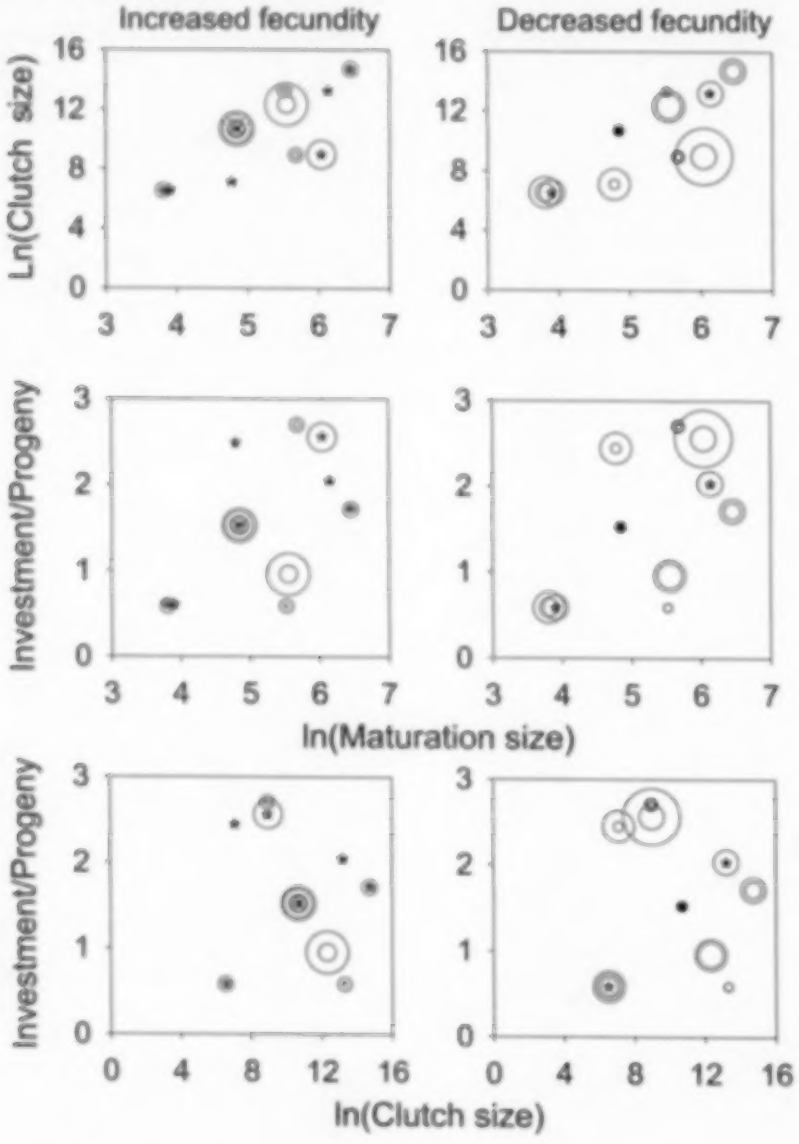
Fig. 10. Scatterplots of predicted population responses of the matrix models and IBMs to increased and decreased fecundity for pairwise combinations of the three life history traits used to define the Winemiller and Rose (1992) life history surface. The size of the symbol is proportional to the absolute magnitude of the predicted response. All responses to increased fecundity were positive (higher average population abundance than baseline) and all responses to decreased fecundity were negative (lower average population abundance than baseline). A star indicates responses ≤15%.



of these below in the spirit of encouraging others to investigate this apparent non-result (see Koricheva 2003).

The first reason for my results could be that the matrix models and IBMs were inappropriate for the analysis. The use of matrix projection models with spawner–recruit relationship for eggs to age 1 seemed reasonable. Indeed, such matrix models are a logical extension of previous analyses that inferred life history influences on population responses (e.g., Barnthouse et al. 1990). Furthermore, age-structured matrix models with spawner–recruit relationships are commonly used in both theoretical analyses (e.g., DeAngelis et al. 1980; Punt 2000) and fisheries management (e.g., Southeast Fisheries Science Center 2002).

Justification of the use of IBMs in this analysis, based on past use of similar models, is more difficult because the IBMs are more complex than the matrix models and they varied greatly in their details. I was involved in the develop-

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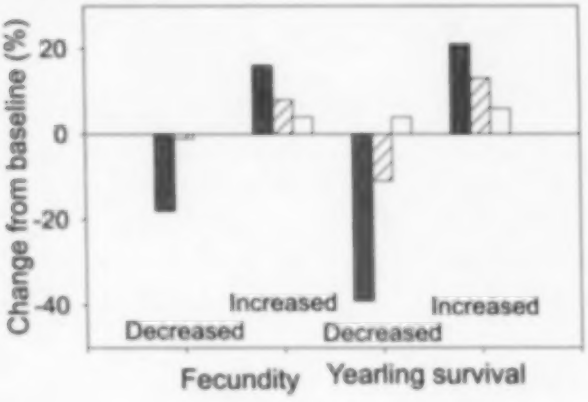
Fig. 11. Predicted population responses (percent change from baseline) for increased and decreased fecundity and yearling survival for the lake trout matrix model with the spawner–recruit relationship only (shaded bars) and with the spawner–recruit relationship and 10% (hatched bars) or 20% (open bars) adult density-dependent growth.



ment of all of the IBMs used, so one would hope that I understood the capabilities of the models and thus did not misuse them in this analysis.

Despite the widespread use of the matrix model and my familiarity with the complex IBMs, it is possible that both types of models were not sophisticated enough to capture important species differences to enable population responses to be related to life history traits. Spatial heterogeneity and density-dependence are two areas that the models likely oversimplified. All of the matrix models represented a single well-mixed box, and many of the IBMs represented one or only a few spatial boxes. The exception was the brook trout model, which represented many habitat boxes of a small stream. Clark and Rose (1997*c*) showed that density-dependent reproduction, growth, and mortality in the brook trout IBM were tightly coupled to the explicit representation of space and the movement of individuals among the spatial boxes. The interaction between density-dependence and spatial heterogeneity has been discussed for fish (e.g., MacCall 1990), and remains an area of much discussion in ecology (Hixon et al. 2002). Furthermore, important differences among species responses could be related to density-dependence in post-young-of-the-year life stages. For example, density-dependent growth of adults, and its effect on reproduction, have been documented in variety of fish species (Helser and Almeida 1997; Rose et al. 2001; Lorenzen and Enberg 2002).

I initially attempted to use a more general form of the matrix projection model (based on stage or stage within age), with density-dependence and stochasticity in all appropriate life stages. I was unable to develop such models for more than a few species, and even those models were based on too much conjecture to ensure that species differences in responses were real or simply a result of my subjective decisions during model development. Nevertheless, including realistic levels of adult density-dependent growth in the lake trout matrix model significantly affected predicted population responses, and showed the potential importance of density-dependent processes outside of the first year of life. While many of the IBMs allowed for density-dependence in the adult life stages, perhaps too few IBMs were used in this analysis to show clear patterns. More sophisticated matrix projection models, especially those having better representation of spatial heterogeneity and density-dependence of adult life stages, and additional IBMs might be needed to clarify the relationship between population responses and life history traits.

A second explanation for the lack of consistent results is that I may have made mistakes in the analysis. Assuming that the matrix models and IBMs were adequate and appropriate for the analysis, I may have done the analysis in a way that masked an underlying relationship between population responses and life history traits. Perhaps I did not standardize the population states appropriately, so species responses were confounded with populations being in different states. While the patterns of responses in the matrix models were similar across SS_{MSR} values, the magnitude of responses to changes in fecundity did depend on population state. The magnitude of responses is important when matrix-model results are mixed with IBM results. Masking of relationships by mixing matrix-model and IBM results is possible but seems unlikely. Matrix-model responses to changes in yearling survival were insensitive to population state, and responses to changes in yearling survival did also not show any patterns in life history space. Furthermore, when I substituted the predicted responses obtained from the matrix models based on 5% SS_{MSR} with the results based on the arbitrary and 10% and 25% SS_{MSR} population states, I again did not find any obvious clustering of small or large responses on the life history surface.

Other aspects of the analysis where I could have gone wrong were in making incorrect assumptions concerning the values of the life history traits and how the changes in fecundity and yearling survival were imposed. These are also possible, but I think unlikely, explanations. I used the life history traits reported in Winemiller and Rose (1992), which may not accurately reflect the life history traits of the actual populations represented in the models. I replotted Figs. 8–10 using the fecundity (mean batch size) and maturation size derived from the matrix-model inputs and IBM simulations; investment per progeny did not change because egg size and parental care were not dependent on model inputs. Very similar non-patterns of responses in life history space were obtained. Use of other values of species' life history traits would reshape the surface, but likely not re-sort the larger or smaller responses towards a particular region of the surface.

It is also possible that the changes in fecundity and yearling survival were not imposed consistently between the matrix model and IBMs. Perhaps larger changes would have resulted in a clearer pattern of responses. I repeated the matrix-model and IBM analyses with 10% and 40% changes in fecundity and yearling survival and obtained results similar to those based on 25% changes. Given the straightforward way in which changes were imposed and the wide range of responses predicted by both types of models, I do not see obvious problems in how fecundity and survival were changed.

The third possible explanation relates to the three-end-point life history surface. Perhaps species' life history strategies

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nicely map onto the Winemiller and Rose (1992) surface, but this does not mean that the magnitude of population responses to changes in survival and fecundity necessarily map onto the same surface. The Winemiller and Rose life history surface is appealingly simple, but may not be appropriate for quantitatively relating life history strategies to population responses. The magnitude of density-dependence in a population is fundamental to determining the population's response to changes in survival. Rose et al. (2001) showed that the steepness of the spawner–recruit relationship, which measures the magnitude of density-dependence, showed wide variation when grouped into the three endpoint strategies of Winemiller and Rose.

Perhaps I needed to correlate the responses to life history traits other than the three (maturation, fecundity, parental care) that define the Winemiller and Rose (1992) life history surface. For example, Schaaf et al. (1987) related population responses to an index of reproduction based on the mean and standard deviation of reproductive contributions by age, and Parent and Schriml (1995) included piscivory in their suite of life history traits to help determine fish species at risk of extinction.

I tried, with only moderate success, several correlation analyses using my predicted responses and a variety of life history traits. For example, I correlated predicted responses by the matrix models to the life history traits of mean age of the population, age at maturity, longevity, number of eggs per mature adult, first-year survival rate, and steepness of the spawner–recruit relationship, all estimated from the baseline matrix-model simulations. Predicted matrix-model responses to changes in fecundity were correlated with steepness ($r^2 \approx 0.8$) but not with any of the other life history traits. Given that the only density-dependence in the matrix model was in the spawner–recruit relationship, this result was expected and not especially useful in data-poor situations that likely would lack spawner–recruit data. Predicted responses to reduced yearling survival were moderately correlated with longevity ($r^2 \approx 0.5$), but responses to increased yearling survival were moderately correlated with mean number of eggs per mature adult ($r^2 \approx 0.5$). I also added the predicted responses from the IBMs to the matrix-model results. I derived average values of five of the same life history traits (not steepness) from baseline simulations of the IBMs, even allowing for different values for the six yellow perch versions, and the correlation results remained murky. Perhaps including additional species in the analysis would help identify the elusive life history traits that are cleanly related to population responses.

The fourth and final possible explanation for my results is that population responses may have a strong site-specific component. Perhaps the models and the analysis were adequate, but the responses of the populations were dominated by the site-specific aspects of each of the models (e.g., Rose and Cowan 2000). The shape of the spawner–recruit relationships used in the matrix models, which was the only density-dependent aspect of the matrix projection models, was critical to the magnitude of responses predicted. I purposely selected spawner–recruit data from specific locations so that the estimated Beverton–Holt relationships were more easily defensible. The IBMs were also developed using data from one or a few similar locations. Perhaps the responses predicted by the models have a strong population (site-specific) component. If this is so, then inclusion of many more populations would enable me to observe the species-level patterns in the responses. Unfortunately, while there are hundreds of spawner–recruit data sets (e.g., Myers et al. 1995), the vast majority involve spawners or recruits reported on relative scales, and involve mostly periodic strategists (Rose et al. 2001). The availability of long-term, absolute-scale spawner–recruit data, especially involving equilibrium- and opportunistic-strategy species, is quite limited. Some candidate equilibrium and opportunistic species that have sufficient spawner–recruit data that could be included in future analyses are the brown trout (*Salmo trutta*) (Elliott 1994; Bell et al. 2000), Pacific sardine (*Sardinops sagax*) (Jacobson and MacCall 1995), alewife (*Alosa pseudoharengus*), and blueback herring (*Alosa aestivalis*) (Jessop 1990). Other IBMs (e.g., Wang 1998) are also available that could be added to the analysis.

Life history has been invoked previously to infer fish population responses to changes in their vital rates (e.g., Jennings et al. 1998; Rochet 2000). Many of these studies were either qualitative, used a limited of species, or made simplifying assumptions concerning density-dependent processes. I assembled a suite of matrix models and individual-based models that addressed these limitations. My analysis did not yield any obvious relationships between the magnitude of population responses and life history traits.

The lack of obvious patterns in the results could be explained by inadequate population models, incorrect analyses, inappropriate life history model, or important site-specific factors. In the case of incorrect analyses and an inappropriate life history model, the problem may be solved with additional empirically based and theoretical analyses, likely performed by others taking a fresh look at the problem. The explanations in terms of inadequate population models and important site-specific influences are more problematic. Both of these explanations have broader implications. Inadequate population models are troublesome because age-structured approaches (e.g., matrix models) with spawner–recruit relationships are widely used (e.g., Barnthouse et al. 1990; Restrepo and Legault 1998), and IBMs are continuing to gain popularity (DeAngelis et al. 1994; Grimm 1999). If site-specific factors play at least a partial role, then my results imply that predictions based on life history theory should remain qualitative, and that quantitative predictions should be based on site-specific data. Some progress on the issue of the role of site-specific factors is possible using multiple populations of a few well-studied species (e.g., Shuter et al. 1998), but such data being limited to a relatively few species will preclude definitive conclusions. Whether adding many more populations to the analysis presented in this paper would allow at least semiquantitative predictions with only minimal site-specific data remains to be determined.

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Regular papers

Articles ordinaires

Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability

David M. Kaplan and Louis W. Botsford

Abstract: The size and configuration of marine reserves best suited to reaching fisheries and conservation goals are poorly understood. It has been suggested that variable spacing between reserves is essential to the success of a system of marine reserves. We used numerical models to examine the effect of variable spacing on the efficacy of marine reserves for managing a fish species with sedentary adults and planktonic larvae. Variability in reserve spacing affected catch and recruitment relative to values for a uniform configuration of reserves only for populations near collapse even in the presence of a system of reserves. For species with low fishing rates or large marine reserves, variability in spacing had only a minor effect. At high fishing rates and small reserve sizes, variable reserve placement had a positive local effect on catch and recruitment when several reserves fell close to each other. These configurations led to uneven spatial distributions with greater catch and recruitment in areas with a higher concentration of reserves. Variable reserve spacing can offer additional protection to overfished populations along certain sections of the coastline, but concern for spatial homogeneity will argue for a uniform distribution of reserves covering an adequate proportion of the entire coastline.

Résumé : On connaît mal les tailles et les configurations des réserves marines requises pour atteindre les objectifs de la pêche commerciale et de la conservation. Il a été suggéré qu'un espacement variable entre les réserves est essentiel au succès d'un réseau de réserves marines. Nous avons utilisé des modèles numériques pour étudier les effets de l'espacement variable sur l'efficacité des réserves marines pour l'aménagement d'une espèce de poisson à adultes sédentaires et à larves planctoniques. La variabilité de l'espacement des réserves affecte les captures et le recrutement différemment d'une configuration uniforme de réserves, seulement chez les populations s'approchant de l'effondrement malgré la présence d'un système de réserves. Chez les espèces affectées par de faibles taux de pêche ou situées près de grandes réserves, le placement variable n'a qu'un effet mineur. Aux taux de pêche élevés et en présence de petites réserves, le placement variable des réserves a un effet local positif sur les récoltes et le recrutement lorsque plusieurs réserves se retrouvent près l'une de l'autre. Ces configurations mènent à des répartitions spatiales inégales avec des récoltes et un recrutement élevés dans les régions à plus fortes concentrations de réserves. L'espacement variable des réserves peut ajouter une protection supplémentaire aux populations surexploitées dans certains secteurs de la côte, mais le souci d'une homogénéité spatiale militera pour une répartition uniforme des réserves couvrant ainsi une proportion adéquate de toute la côte.

[Traduit par la Rédaction]

Introduction

Although protected areas have been common practice in terrestrial systems since the beginning of the twentieth century, it is only recently that there has been an intense effort in many parts of the world to institute systems of coastal marine reserves for conservation and fisheries management. It has been suggested that reserves are a more efficient way to manage certain marine resources than traditional effort-based management (e.g., Plan Development Team 1990; Dugan and Davis 1993; Bohnsack 1998). The design of systems of marine reserves provides unique challenges different from those seen in terrestrial systems (Hockey and Branch 1994; Simberloff 2000; Carr et al. 2003). This is primarily due to the predominance of marine species with sedentary adult phases and widely dispersing larval phases. Moreover, marine reserves have to satisfy two often-competing measures of performance: for conservation, ecosystem sustainability is the primary goal, while for fisheries, high catch and sustainability of harvested species are desired.

There is a growing body of literature that addresses spatial aspects of marine reserve design. Some have focused on developing rules for choosing configurations that maximize biodiversity, maximize habitat heterogeneity, and (or) include vulnerable habitats, life stages, or species within reserves (e.g., Hockey and Branch 1997; Leslie et al. 2003; Roberts et al. 2003). While these reserve-siting schemes are needed to create reserves with the appropriate selection of desired habitats, species, and ecosystems, they do not specify the combination of reserve locations, sizes, and spacings necessary for species sustainability and high fisheries yields. These issues have been addressed primarily through modeling efforts that identify the factors that are important for determining the size and configuration of marine reserves (see Gerber et al. 2003 and references therein). Here, we

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D.M. Kaplan[1] and L.W. Botsford. Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616, USA.

[1]Corresponding author (e-mail: dmkaplan@ucdavis.edu).

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build on this literature by examining the effect that variability in the spacing of reserves along a linear coastline has on the sustainability and yield of a coastal marine species with a planktonic larval phase and sedentary adults. Species that have this type of life history include most benthic invertebrates, most rockfish, and some reef fish. These are among the species most threatened by overfishing, and they are the most likely to benefit from the implementation of marine reserves.

One factor that has been identified as important for determining the size and spacing of reserves required for persistence is larval dispersal distance. Botsford et al. (2001) created a population model for a species with sedentary adults and dispersing larvae with a system of uniformly spaced marine reserves, complete removal of adults outside reserves by fishing, and Laplacian dispersal patterns. They showed that a species persists in any single reserve that is at least as large as the species' average dispersal distance. Furthermore, species with any dispersal distance would be sustained by a system of marine reserves that covered at least a minimum fraction of the entire coastline. In their model, that minimum fraction is the same as the fraction of natural (unfished) lifetime egg production required for a population to persist, which is often taken to be 35% (cf. Mace and Sissenwine 1993). These results have been extended to combinations of reserves and fishing removal rates that provide sustainability along noninfinite coastlines (D.R. Lockwood et al., Center for Population Biology, Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616, USA, unpublished data). Actual dispersal distances of relevant species are poorly known. It has been shown that they vary greatly between species (Grantham et al. 2003; Kinlan and Gaines 2003; Shanks et al. 2003), although recent empirical results indicate that local retention of larvae might be much more common than once thought (e.g., Todd 1998; Warner et al. 2000; Mora and Sale 2002).

The above-mentioned results that assess reserve configurations (i.e., Botsford et al. 2001; Gaines et al. 2003; D.R. Lockwood et al., Center for Population Biology, Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616, USA, unpublished data) are based on idealized, evenly spaced systems of reserves applied to fish populations with sessile adults. However, as a practical matter, it is unlikely that a uniform distribution of marine reserves will be implemented in the real world. Furthermore, some have suggested that nonevenly spaced reserves could better protect fish populations with a variety of dispersal distances (e.g., Palumbi 2002). For these two reasons, there has been considerable interest recently in the consequences for fisheries yield and marine conservation of creating systems of reserves with nonuniform spacing. In this paper, we address the issue of variability in reserve spacing through a spatially explicit numerical model of marine populations.

The rest of this paper is organized as follows. We begin by describing the model that we used to examine the effects of variable reserve spacing on fish populations. Then, we briefly describe the effect of marine reserves on fish populations in the absence of random reserve placement. We follow that by presenting results on sustainability and catch with random reserve placement. Finally, we summarize the results and place them in the larger context of marine reserve design in the discussion.

Methods

We studied the effects of random reserve placement using a spatially explicit, size- and age-structured model with a monthly time step, similar to that used in Botsford et al. (1999) and Lockwood et al. (2002). It consisted of 100 independent, size-structured subpopulations placed along a linear coastline connected via dispersal of larvae through a dispersal matrix. The length of coastline occupied by each subpopulation will be referred to as a "spatial unit" throughout this paper. Because dispersal distance is given in the same units, the actual units are arbitrary.

Adults in each subpopulation were subject to growth, natural and possibly fishing mortality, and size-dependent reproduction. With the exception of fishing mortality, all population parameters affecting adults were identical in each subpopulation and were similar to those used in Botsford et al. (1999). Values were based on those found for the red sea urchin (*Strongylocentrotus franciscanus*) along the coast of northern California (Morgan 1997). The red sea urchin is a slow-growing, benthic invertebrate that has widely dispersing larvae. It is known to be susceptible to overfishing and is considered to be a good candidate for management through the use of marine reserves (Kalvass and Hendrix 1997; Botsford et al. 1999; Morgan et al. 1999). Although the population parameters used in the model are species specific, we focus here on those general trends that are robust to changes in parameter values. The results presented here are applicable to a wide class of marine species with relatively sedentary adults, including most benthic and intertidal invertebrates, as well as rockfish and some coral reef fish. The entire set of parameter values is provided in Table 1.

Growth of individuals in each subpopulation was governed by a von Bertalanffy equation with Gaussian distributed variability in maximum size (Ricker 1975; Smith et al. 1998). Individuals in the model were allowed to live for a maximum of 30 years. In the absence of fishing, mean age of individuals in the model was 9.6 years. Beverton–Holt postsettlement density dependence of juveniles was included in the model (Beverton and Holt 1957). The value of a, the slope of the larvae–recruit curve at the origin, was set so that the population collapsed (i.e., population size eventually went to zero) when lifetime egg production was less than 35% of its unfished value. Thirty-five percent lifetime egg production was chosen as a convenient and oft-quoted reference point. The exact value used is not crucial for the results discussed here. This value produced collapse of the population at a fishing rate of 0.11·year^{-1} in the absence of marine reserves. Fishing mortality rate was identically zero inside reserves with knife-edge selection at the boundaries. This implies that adults are sedentary and do not cross reserve boundaries, an acceptable approximation as long as the spatial scale of adult movement is considerably smaller than the size of reserves (Nowlis and Roberts 1999).

A dispersal matrix related the density of presettlement larvae along the coast to the final density of competent larvae that settle into each subpopulation. A Laplacian dispersal kernel was used, which exponentially decays with distance

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Table 1. Parameter values for the population model.

Parameter name	Symbol	Value
Recruitment		
Slope of Beverton–Holt density dependence	a	0.006 62
Juvenile carrying capacity	C	12 000 000
Growth		
Maximum size	L_∞	118 mm
Standard deviation of maximum size	σ	10 mm
von Bertalanffy growth parameter	k	0.22
Reproduction		
Size of first reproduction		60 mm
Reproduction coefficient	a	5.47×10^{-6}
Reproduction exponent	b	3.45
Mortality		
Natural mortality rate	m	0.08·year^{-1}
Fishing size limit		60 mm
Fishing mortality rate	f	*0.05–0.2·year^{-1}*
Reserve configuration		
Number of reserves		4
Reserve size		*5 or 10 spatial units*
Dispersal		
Dispersal distance		*1–25 spatial units*

Note: Italics indicate parameter values that varied between model runs. All others were held constant.

in both alongshore directions. The average distance that settling larvae were from the point of reproduction, here referred to as the "dispersal distance", was constant over space and varied from 1 to 25 spatial units. We also considered the case of a larval pool, where larvae are evenly redistributed across subpopulations. This is essentially equivalent to an infinite dispersal distance. Circular boundary conditions were used, so larvae reaching one edge of the model system simply reappeared at the other edge. This essentially simulates an infinite coastline. We chose to use circular boundary conditions so as not to confound the effects of reserve placement with edge effects due to finite habitat length.

For each run of the model, the system was started at equilibrium in the absence of fishing and marine reserves. Then, fishing and marine reserves were introduced and the model was run for an additional 100 years. After that, because the system approached equilibrium very slowly, model results were fit by least-squares to an exponential decay to obtain final equilibrium values of catch and recruitment.

Two types of variability in reserve spacing were considered. In the first type, which we call the "jitter" case, reserve placement was continuously perturbed from the uniform configuration (Fig. 1). With no jitter, the system consisted of four uniformly spaced reserves. With jitter, each reserve could shift position by up to a specified number of spatial units while maintaining reserve size constant. Each reserve shifted independently of all other reserves. The number of spatial units shifted by an individual reserve was randomly determined with equal probability for all values between zero and the specified jitter value. By increasing the amount of jitter, we were able to explore population dynamics for systems with increasingly variable reserve spacing. In the second type of variability in reserve spacing, the placement of reserves was completely random, with the condition that reserves be nonoverlapping. These two configurations will be presented together, with the totally random case being considered an extreme case of jitter. Ten model runs were performed for each fishing rate, reserve size, and level of variability in reserve spacing. These runs were then compared with a model with the same fishing rate and reserve size but a uniformly spaced configuration of reserves.

Fig. 1. Depiction of "jitter" in marine reserve design. Reserves are indicated by solid boxes. Possible alternate positions for the reserves are shown by open boxes. The example shown has a jitter of four spatial units. Each reserve is allowed to appear randomly in one of five positions. Reserve size is held constant. The figure demonstrates two of the five possible reserve positions.

Results

Uniform reserve placement

We first summarize the results for the case of uniform reserve placement, against which random reserve placement is compared. Without reserves, the system collapses at a fishing rate of approximately 0.11·year^{-1} and dispersal distance has no effect on population dynamics (Fig. 2). Maximal sustainable yield in the absence of reserves occurs at a fishing rate of 0.05·year^{-1}. When reserves are added, the fishing rate in nonreserve subpopulations at which maximal sustainable yield occurs increases with the size of the marine reserves introduced (Fig. 2*b*). The maximal sustainable yield is greatest in the absence of reserves, although the range of fishing rates for which catch is relatively high is wider when the system includes marine reserves.

With reserves, maximal sustainable yield also depends on dispersal distance, with the greatest yields being produced at intermediate dispersal distances (relative to the size of the reserves, 5 or 10 spatial units in our model; Fig. 2*b*). Extremely short-distance dispersers show both lower yields (Fig. 2*b*) and lower recruitment (Fig. 2*a*), relative to species with larger dispersal distances, owing to poor export outside of reserve areas, while long-distance dispersers have intermediate to low levels of recruitment and catch. The effect of dispersal distance is strong: minimum recruitment levels in the model with reserves of five spatial units each and a fishing rate of 0.2·year^{-1} represent about 50% of the maximum level.

Although the focus of this paper is on the population state after reserves are created, the results in Fig. 2 can be used to make a comparison between management with reserves and effort-based management alone. Two possible scenarios for the redistribution of fishing effort after reserves are created are removal of fishing effort by marine reserves and conservation of total fishing effort before and after reserves are created. Reserves reduce catch relative to effort-based management alone at low prereserve fishing mortality rates (Fig. 3*a*) but increase catch at high prereserve fishing mortality rates (Fig. 3*c*), as noted by several other authors (e.g., Bohnsack 1998; Hastings and Botsford 1999; Nowlis and

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Fig. 2. Equilibrium values of (*a*) recruitment and (*b*) catch for a system of uniformly spaced reserves as a function of dispersal distance (spatial units (SU)) and fishing rate. The darkest surface is the result for the population without any reserves, the medium-gray surface is for a system with four reserves of five spatial units each (20% coverage by reserves), and the lightest surface is for a system of four reserves of 10 spatial units each (40% coverage by reserves).

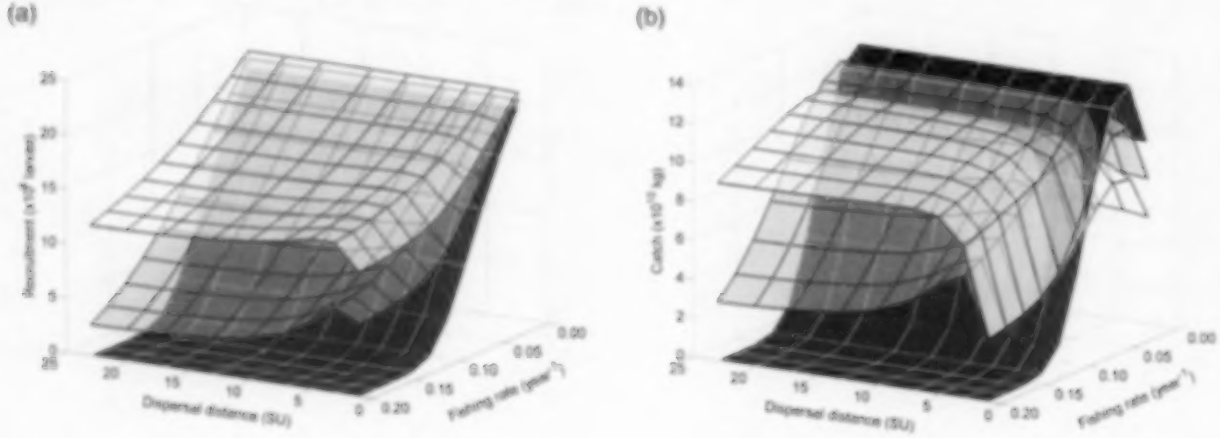
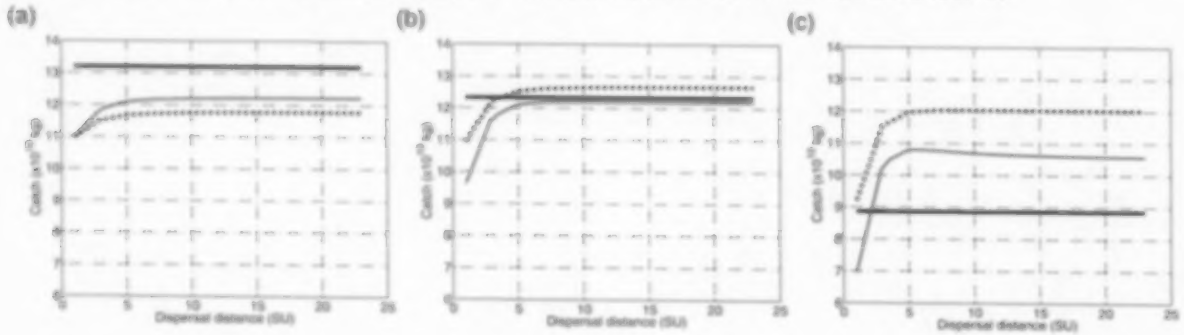


Fig. 3. Equilibrium catch levels as a function of dispersal distance (spatial units (SU)) for prereserve fishing mortality rates of (*a*) 0.04·year^{-1}, (*b*) 0.06·year^{-1}, and (*c*) 0.08·year^{-1}. The thick solid lines are for the system in the absence of marine reserves. The broken lines are for a system of four uniformly spaced reserves of five spatial units each (20% of total habitat in reserves) when total fishing effort is not conserved (i.e., the fishing mortality rate in nonreserve areas is the same as the prereserve fishing mortality rate). The thin solid lines are for an identical system of marine reserves when total fishing effort is conserved (i.e., the fishing mortality rate in nonreserve areas is the prereserve fishing mortality rate divided by the fraction of the total area not in reserves).



Roberts 1999). Conservation of total fishing effort generally reduces the absolute difference between yield with reserves and without. In particular, at high prereserve fishing rates, the potential gains when reserves are created are reduced if effort is conserved (Fig. 3*c*). On the other hand, for prereserve fishing rates above 0.11·year^{-1} (not shown), the population without reserves went to extinction, while systems with reserves persisted until quite high fishing rates even if total fishing effort was conserved.

In the following analysis of the effects of random reserve placement, we will refer to the fishing mortality rate in nonreserve areas without reference to how it relates to the prereserve fishing rate, as our focus is on comparing systems with different spatial configurations of marine reserves.

Random reserve placement

We tested the effect of random reserve placement on the model with fishing rates in nonreserve areas of 0.05, 0.1, and 0.2·year^{-1} and four reserves of 5 or 10 spatial units each (20% or 40% of total area in reserves). Over most values of dispersal distance and jitter, the effect on recruitment and catch was relatively small (Fig. 4), particularly when viewed in the context of the variation caused by dispersal distance, which significantly affected both catch and recruitment (Fig. 2). In the vast majority of runs, jitter and random reserve placement resulted in less than a 5% change in catch and recruitment relative to the system with uniformly spaced reserves. In the most extreme cases of random reserve placement examined, recruitment increased by about 75% over the same system with uniformly spaced reserves, and catch increased by 45%.

Three principal trends are evident in the results: (*i*) the effect of variable reserve spacing on recruitment and yield was greatest in the least persistent cases (note that scales on the vertical axes vary), (*ii*) the effect tended to be positive for longer dispersal distances and negative for shorter dispersal

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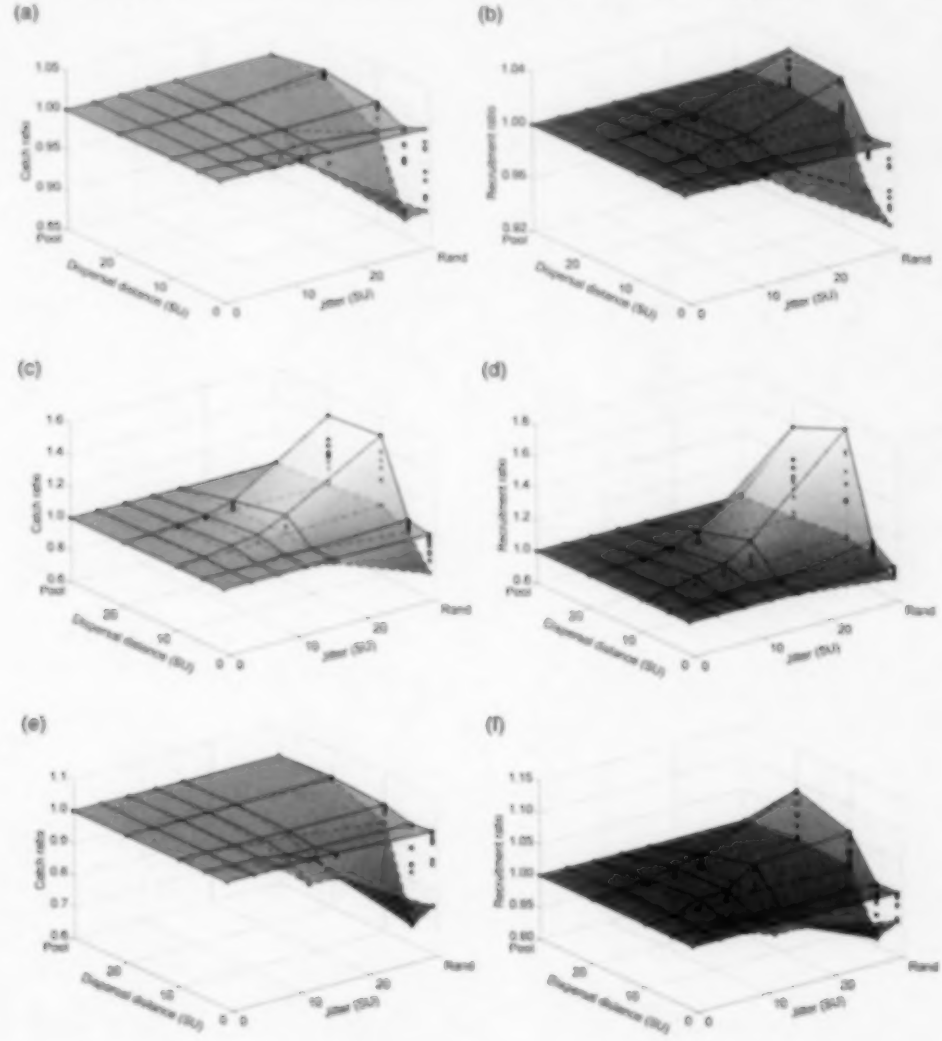
Fig. 4. Equilibrium catch and recruitment for a variety of fishing rates as a function of dispersal distance and "jitter" (spatial units (SU)). Results have been normalized by the value for a uniform distribution of reserves for each dispersal distance. Surfaces are maximum and minimum values for each set of 10 runs, with individual runs indicated by circles. "Rand" indicates runs that had a completely random distribution of reserves. "Pool" indicates that larvae were dispersed uniformly to all subpopulations, the equivalent of an infinite dispersal distance. (*a*) Catch for a fishing mortality rate (f) of 0.1·year^{-1} and reserve size (RS) of five spatial units; (*b*) recruitment for f = 0.1 and RS = 5; (*c*) catch for f = 0.2 and RS = 5; (*d*) recruitment for f = 0.2 and RS = 5; (*e*) catch for f = 0.2 and RS = 10; (*f*) recruitment for f = 0.2 and RS = 10. Note that the vertical scale is different in each panel.



distances, and (*iii*) the effect on recruitment was generally positive, but the effect on catch was positive only in the least persistent case. With regard to the first trend, variable reserve spacing produced higher values of catch and recruitment than a uniform configuration of reserves when the fishing rate was high (Figs. 4*a* and 4*b* versus 4*c* and 4*d*) or reserve size was low (Figs. 4*e* and 4*f* versus 4*c* and 4*d*), both of which tend to move the system towards collapse (Fig. 2). This effect is most evident in the system with reserves of five spatial units each and a fishing rate of 0.2·year^{-1} (Figs. 4*c* and 4*d*). In this case, recruitment was as much as 75% higher with random reserve placement. Note, however, that at a fishing rate of 0.2·year^{-1} and mean dispersal distance of 10–20 spatial units, this is 75% of a fairly low recruitment rate.

With regard to the second trend, for species with dispersal distances less than five spatial units, random reserve placement reduced both catch and recruitment in all cases. For longer dispersal distances, variability in reserve spacing generally increased recruitment but only increased catch when the fishing rate was 0.2·year^{-1} and the reserve size was five spatial units, the case closest to collapse. At extremely long

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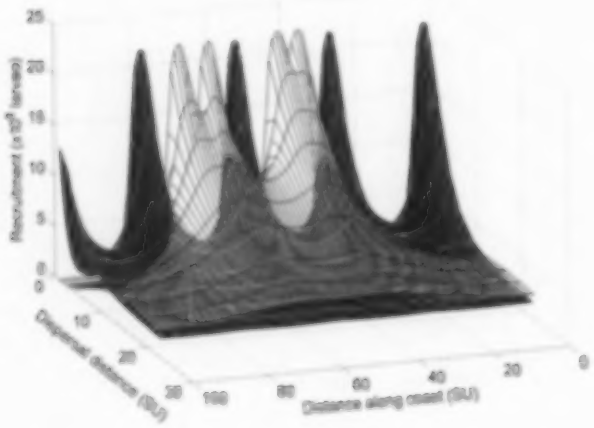
Fig. 5. Spatial pattern of equilibrium values for recruitment as a function of dispersal distance (spatial units (SU)) for uniform and nonuniform distributions of marine reserves at a fishing rate of 0.2·year^{-1}. The solid surface is recruitment for a system that has four evenly spaced reserves, while the open surface is for a system that has four unevenly spaced reserves. Each of the reserves is five spatial units wide. The nonuniform distribution is the configuration of reserves that resulted in the highest values of catch and recruitment for that fishing rate and reserve size. Note that recruitment for the uneven distribution of reserves remains nonzero in the center of the domain even for large dispersal distances but collapses along the edges where there are no reserves. Recruitment for the even distribution of reserves collapses for all but the smallest dispersal distances.



dispersal distances (the "pool" case, the upper left-hand margin of each plot), spatial configuration is no longer relevant to population dynamics.

Configurations producing extreme values

We examined in greater detail those reserve configurations that produced significant changes in catch and (or) recruitment for a reserve size of five spatial units and fishing rate of 0.2·year^{-1}. These parameter values were chosen because they are illustrative of species that are not well protected by a single reserve for intermediate to large dispersal distances because of larval dispersal outside the reserve and overfishing, a case that is likely to be of interest in real marine reserves given the relatively long dispersal distances of some important species (Kinlan and Gaines 2003; Shanks et al. 2003), the size restrictions placed on potential marine reserves, and the heavily fished state of many of the world's fisheries (Botsford et al. 1997; Hutchings 2000).

Under these conditions, a nonuniform distribution of reserves had higher levels of both catch and recruitment than a uniform distribution in cases where reserves of the system randomly happened to be concentrated along a relatively short piece of coastline (e.g., Fig. 5). Recruitment would have collapsed for anything but the smallest dispersal distances in the corresponding system with a uniform distribution of reserves, but several closely spaced reserves maintained high recruitment levels in and around the reserves even for large dispersal distances. The nonuniform distribution of reserves, however, had extremely low levels of recruitment along those parts of the coastline that had few reserves, particularly at short dispersal distances.

Discussion

Variable spacing between marine reserves has a relatively minor effect on catch and recruitment of larvae in populations that would be far from collapse with a uniform distribution of marine reserves, i.e., those with low fishing rates and (or) large reserves. Both jitter and completely random reserve designs tended to perform poorly when compared with a uniform distribution of marine reserves for persistent populations, although the effect was quite small. This small decrease in catch and recruitment is attributable to saturation of larval settlement inside marine reserves. Postsettlement density dependence places a maximum on the number of larvae that can settle successfully in a subpopulation each year. Potential settlers above this maximum do not increase the number of successfully settling larvae. As a result, in persistent populations, larvae that disperse from one reserve to another reserve do not contribute to the adult population and it is beneficial to export as many larvae as possible from reserves to fished areas. With a decaying dispersal pattern, this is achieved by a uniform distribution of reserves.

In populations that are not persistent or are near collapse with uniformly spaced reserves (high fishing rates and dispersal distances greater than reserve size), variable spacing of reserves can increase local population density relative to the uniform case. The effect can be quite large. In collapsing populations, small changes in protection of an area along the coastline can make the population locally persistent and thereby produce large changes in the overall population (when compared with the low recruitment levels produced by overfished populations). For high fishing rates and a system of small reserves, species with dispersal distances larger than the reserve size are not sufficiently protected to ensure persistence with a uniform distribution of reserves (Botsford et al. 2001). By instituting variable spacing in a system of marine reserves, some reserves naturally fall close together and protect more than 35% of the reproductive output in that local area, producing a network of reserves that is locally self-sustaining for intermediate distance dispersers. This saves the population from complete collapse and produces higher catches and recruitment in and around the reserves. Nevertheless, in this scenario, large areas of coastline have no marine reserves and necessarily the population collapses in those areas.

These results suggest that varying the spacing of marine reserves along the coastline could have a benefit for those species that are most threatened by overfishing. If there is concern that reserves will not cover an adequate percentage of the entire coastline to ensure persistence for all species, a higher percentage of the coastline could be covered over a limited area. However, that would be at the expense of the fraction covered in other areas. Furthermore, nonuniform reserve spacing produces an uneven distribution of catch and is unlikely to please anyone but fisherman living near the area of higher reserve density. The political ramifications of this uneven distribution could potentially outweigh any benefit derived from an uneven distribution of reserves.

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Our results are consistent with the results for a uniform distribution of reserves (Botsford et al. 2001). If a single reserve protects all species with dispersal distances less than the size of the reserve, then varying the reserve spacing should only be a benefit to those species with longer dispersal distances. Furthermore, even those species with dispersal distances larger than the reserve size can only receive a significant benefit from variability in reserve spacing if the uniform system of reserves does not cover a sufficient percentage of the coastline to protect all species along the entire coastline.

There are a number of other factors that are potentially relevant to the design of marine reserves for sustainability and yield of fish populations that have not been treated in this study. The functional relationship between size and reproductive output was not varied and overcompensatory density dependence was not considered. Although these factors are important to the issue of whether effort-based management or management with marine reserves is likely to produce the highest yields (Parrish 1999; Berkeley et al. 2004), they are unlikely to significantly alter trends in catch as a function of the spacing between reserves. Furthermore, we have not attempted a complete treatment of how fishing effort might be redistributed after the creation of marine reserves. This process is quite complex and case specific (Beverton and Holt 1957; Wilen et al. 2002; Smith and Wilen 2003). Our results indicate that the potential gains due to the creation of marine reserves for overfished species are likely to be reduced when total effort is conserved. Exactly how fishing effort is redistributed will change the difference between catch from conventional management and catch with reserves, but will not alter our conclusions regarding variable spacing between reserves. Variable spacing can only have an effect if the final fishing rate in nonreserve areas produces a system that is overfished even with marine reserves.

Larval dispersal in our model was symmetric around the point of larval origin and uniformly decreasing with distance. Alongshore advection of larvae was not included in the model. It has been shown that alongshore larval advection can have a significant impact on the efficacy of a system of marine reserves (Gaines et al. 2003). On the other hand, a number of recent studies indicate that larval retention and concentration are relatively common (Todd 1998; Warner et al. 2000; Mora and Sale 2002), even in upwelling-dominated systems where one would normally expect strong alongshore currents (Graham and Largier 1997; Wing et al. 1998). Significant retention suggests that advection distances are likely to be smaller than was once thought and alongshore advection might not play an important role in population dynamics. Nonetheless, one must apply the results in this paper with caution when there exists the possibility of strong alongshore advection.

We also did not consider more complex two-dimensional patterns of larval dispersal, as might be found along convoluted coastlines and groups of islands, for example. These conditions will change the connectivity between adult subpopulations and therefore could have important consequences for the design of systems of marine reserves. Given the complexity of possible two-dimensional configurations of dispersal patterns and marine reserve designs, we have limited ourselves here to a linear coastline. We speculate that the trends found here regarding variability in reserve spacing would not differ significantly if two-dimensional reserve configurations were considered.

Adult movement and "spillover" from reserve boundaries were not included in our model. This is a reasonable approximation if the size of reserves is considerably larger than the spatial scale of adult movement (Nowlis and Roberts 1999), as one would expect for species with low mobility (e.g., many marine invertebrates) and (or) small territorial ranges (e.g., most rockfish). If adults are migratory or have large territories, reserves will only offer them protection for the percentage of the time they spend inside reserves. In this case, the distinction between reserve and fishing areas is much less clear. The results of our model would only be applicable to the extent that reserves provide a real decrease in local fishing pressure.

All habitats in our model were considered equally suitable for settlement of larvae and adult survival in the absence of fishing. Here, it is assumed that the scale of habitat variability is smaller than an individual spatial unit and that all spatial units have roughly an equivalent percentage of habitable terrain. One might expect to satisfy these conditions for sufficiently large sections of the coastline in the middle of a species' range. Species domain boundaries, large areas of unsuitable terrain, and large-scale variability in terrain habitability will undoubtedly complicate population dynamics, but it is likely that several closely spaced reserves will continue to locally benefit overfished species along that section of the coastline.

Ultimately, the actual distribution of marine reserves will be determined by a mixture of science and political feasibility. It is unlikely that an extremely nonuniform distribution of reserves could be implemented because of the short-term negative effects on local fishermen of closing sections of the coastline to fishing in areas where reserve density is high. To lessen the impact on any one group of fishermen, it is probable that reserves will tend to be approximately uniformly spaced along the coast. This study indicates that small divergences from uniform reserve spacing are unlikely to have a large positive or negative impact on population size. However, there is one case in which an uneven distribution of reserves may actually be acceptable to stakeholders. There has been some discussion of partial implementation of a system of reserves as a way of demonstrating their benefits as they are "phased in". Our results indicate that if the purpose of placing only a small fraction of the coast in reserves were to demonstrate the benefits of marine reserves, then that fraction should be concentrated in an area on the order of the dispersal distance of the species to be protected rather than distributed evenly along the coast.

Acknowledgments

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Resource matching across habitats is limited by competition at patch scales in an estuarine-opportunist fish

Karl M. Polivka

Abstract: I used field observations, assays, and experiments with the euryhaline cottid *Cottus aleuticus* to evaluate the extent to which average resource availability drives the large-scale distribution of these fish among upstream and estuarine habitats and how interspecific competition from a congener affects its performance in the estuary. Population densities of *C. aleuticus* were only consistent with resource densities across years during two of five study years, indicating a lack of resource matching at large temporal scales. On shorter temporal scales, fish growth rates that were two to three times higher in the estuary compared with the stream were inconsistent with the predictions of resource matching theory. A manipulation of *C. aleuticus* density showed that the estuary could support at least twice the number of individuals that occurred there; thus, the profitable estuary is underutilized. Interspecific competition with *Cottus asper* was partially responsible for this underutilization as indicated by a substantial reduction in growth and condition among *C. aleuticus* individuals in experimental manipulations that compared intra- and inter-specific effects. Observed spatial overlap between these two cottids combined with the results of the competition experiment suggests that *C. aleuticus* is more strongly limited in its ability to use estuarine habitats opportunistically by interspecific competition than by intraspecific competition.

Résumé : Des observations de terrain, des tests et des expériences avec le cottidé euryhalin *Cottus aleuticus* ont permis d'évaluer en quelle mesure la disponibilité moyenne des ressources explique la répartition à grande échelle de ce poisson dans les habitats fluviaux d'amont et dans l'estuaire et comment la compétition interspécifique par un congénère affecte sa performance dans l'estuaire. Les densités de population de *C. aleuticus* ne correspondent aux densités des ressources que durant deux des cinq années de l'étude, ce qui indique une absence d'appariement des ressources aux grandes échelles temporelles. Aux échelles temporelles plus courtes, les taux de croissance des poissons, qui sont deux–trois fois plus élevés dans l'estuaire que dans les cours d'eau, ne s'accordent pas avec les prédictions de la théorie de l'appariement des ressources. Une manipulation de la densité de *C. aleuticus* montre que l'estuaire pourrait contenir au moins deux fois plus d'individus qu'il n'y en a actuellement; ainsi l'estuaire, un habitat plus avantageux, est sous-utilisé. La compétition interspécifique avec *C. asper* est en partie responsable de cette sous-utilisation; en effet, des manipulations expérimentales qui comparent les effets intraspécifiques et interspécifiques montrent une réduction substantielle de la croissance et de la condition chez *C. aleuticus*. Le chevauchement spatial observé entre ces deux cottidés en plus des résultats des expériences sur la compétition laissent croire que *C. aleuticus* est plus limité dans sa capacité à utiliser de façon opportuniste les habitats de l'estuaire par la compétition interspécifique que par la compétition intraspécifique.

[Traduit par la Rédaction]

Introduction

Heterogeneous environments that differ in profitability among patch or habitat types offer the opportunity for organisms to persist within them through optimal habitat selection and fitness maximization depending on the ability of such organisms to respond to spatial and (or) temporal variation in resource abundance. Existing ecological theory can address the relative resource matching capabilities of organisms that move among habitats and patches. Resource matching is predicted by the ideal free distribution (IFD) (Fretwell and Lucas 1970; Fretwell 1972) and theoretical advances of the IFD model address its relatively simplistic assumptions about the perceptual requirements of foragers (Spencer et al. 1996; Tyler and Hargrove 1997; Ranta et al. 1999), competitive differences among individuals in the population (Spencer et al. 1995; Hugie and Grand 1998; Tregenza and Thompson 1998), and the costs of movement

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K.M. Polivka.[1] Department of Ecology and Evolution, University of Chicago, 1101 E. 57th Street, Chicago, IL 60637, USA.

[1]Present address: USDA Forest Service, Pacific Northwest Research Station, Wenatchee Forestry Sciences Laboratory, 1133 N. Western Avenue, Wenatchee WA 98801, USA (e-mail: kpolivka@fs.fed.us).

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that affect settlement patterns when habitats are occupied by individuals at low density (Greene and Stamps 2001) or emigration costs that may adjust the relative value of apparently better or poorer habitats (Morris 1987*a*).

An IFD-based equilibrium distribution occurs when the proportion of individuals in each habitat roughly matches the proportion of resources available in each and intake rates, individual growth, and survivorship become equal across habitats or patches. These manifestations are collectively referred to as numerical or performance resource tracking at the observed densities in each habitat (Folt et al. 1998). However, if numerical and performance responses do not indicate equilibrium between the two habitats as predicted by the IFD, then the population is likely constrained by other mechanisms that interact with the effects of density dependence.

Field populations typically fail to show numerical and performance responses consistent with the IFD (Kennedy and Gray 1993), and in many cases, perfect resource matching is not expected. Nevertheless, the IFD is an appropriate null model for testing habitat selection under varying habitat features (e.g., Giannico and Healey 1999). The study of fish distributions in estuarine tidal creeks and adjacent stream habitats might benefit from the use of IFD predictions in designing empirical tests in laboratory (e.g., Milinski 1979) or field (e.g., Fraser and Sise 1980; Power 1984; Nislow et al. 1998) settings that elucidate mechanisms that affect the ability of organisms to match the availability of their resources. In this manner, the IFD serves as a tool rather than a hypothesis to examine different consumer–resource systems (e.g., Oksanen et al. 1995) and the lack of an actual IFD motivates further investigation into the processes that negate matching.

Interspecific competition may constrain resource matching when a superior competitor excludes an inferior competitor from exploiting all patches in a habitat. The observed reduction in performance in the presence of a competitor should be as strong as or stronger than that observed in the presence of conspecifics. Under strong competition, stable coexistence depends on the presence of at least one axis of environmental heterogeneity along which species can partition resources (e.g., Connell 1961; MacArthur and Pianka 1966; Rosenzweig 1987). Complete partitioning of resources (e.g., Werner 1977; Werner and Gilliam 1984) or of different physical properties of the environment (e.g., Ross 1986; Matthews 1987; Denno et al. 1995) is predicted for fishes that experience competition on evolutionary time scales. However, overlap of species is frequently observed and might affect the short-term resource matching ability of one species in the zone of overlap (e.g., Weisburg 1986; Costello 1992; Garrison 2000). I will show that ecologically similar species in estuaries experience competitive effects that limit one species' estuarine distribution.

Estuaries are very productive habitats (e.g., Schelske and Odum 1962; Underwood and Kromkamp 1999), and their high productivity is exploited by both freshwater and marine organisms. Fishes that utilize estuarine habitats generally do so during early stages of their life histories and are typically euryhaline species that enter estuaries from marine habitats (e.g., Valesini et al. 1997; Gray et al. 1996) or streams and large rivers with oceanic interfaces (e.g., Blaber and Blaber 1980; Kneib 1984; Limburg et al. 1997). Some marine species, however, are known to enter estuaries as spawning adults (e.g., Yanez-Arancibia and Lara-Dominguez 1988). Most species are not permanent residents, and those that are primarily abundant as juveniles or present on short temporal scales are classified as either estuarine opportunists or stragglers (Lenanton and Potter 1987). Opportunists use estuaries as nursery areas, but it is difficult to determine whether estuarine resources contribute directly to an overall fitness advantage in individuals that use estuarine resources opportunistically. Some studies have considered the role of resource differences between estuaries and upstream habitats in observed distributions of some freshwater species in estuaries and have associated these patterns with experimental evidence that the enhanced foraging opportunities drive estuarine habitat selection (e.g., Frank and Leggett 1986; Sogard 1992; Kneib 1993).

Estuarine-opportunist fishes provide the opportunity to test the strength with which resources influence species distributions in the context of resource matching predictions at large and small spatial scales. In this study, I evaluate whether fish match average resource availability across habitat types (freshwater versus estuarine) and the role of intra- and interspecific competition at the patch scale as mechanisms limiting their ability to do so. The freshwater cottid *Cottus aleuticus* uses both estuarine and upstream habitats, and if resources are the primary mechanism leading to density differences at the habitat scale, then this species should show numerical and performance resource tracking even when average fish density and resource availability are evaluated at the patch scale. I show that fish population and prey resource densities are higher, on average, in an estuary than in the stream above the mixohaline zone. Fish densities did not match resource availability because growth rates in the estuary under increasing intraspecific competition in *C. aleuticus* indicated that the habitat is not saturated as would be the case under the IFD's resource matching equilibrium prediction. Interspecific competition with *Cottus asper* at the patch scale in the estuary significantly reduces both growth and condition factor in *C. aleuticus* to a greater extent than I observed in fish presented with increased densities of conspecifics only and appears to be one mechanism operating to limit the use of estuaries by *C. aleuticus*.

Methods

Study system

Estuaries along the Pacific coast of North America contain juveniles of both marine and freshwater fishes, but assemblages tend to be dominated by marine species, particularly during summer recruitment (e.g., Horn and Allen 1976; Allen 1982; Yoklavich et al. 1991). The coastrange sculpin *C. aleuticus* is abundant in the lower to middle reaches of streams of the Pacific coast from Alaska to southern California (Moyle 1976; Lee et al. 1980). Populations may complete the entire life cycle in fresh water (McLarney 1968; Ikusemiju 1975), use estuaries as nursery areas for juveniles (Ringstad and Narver 1973), or show a "mixed/fluvial" life history pattern (i.e., spawn and raise juveniles in all areas of

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the drainage or spawn in all areas but restrict juveniles to estuaries; Brown et al. 1995).

Cottus aleuticus and *C. asper* are the most abundant estuarine-opportunist freshwater fishes that occur in Big Beef Creek, a low-order stream draining into Hood Canal in the western Puget Sound region of Washington (USA). The stream is about 9 km in length, with the last 0.7 km in the intertidal zone. At high tide, the upstream portion of the mixohaline zone reaches salinity levels of 10–15 ppt, whereas the salinity closer to the mouth of the estuary is 20–25 ppt (K.M. Polivka, unpublished data). At low tide, the water in the active river channel is completely fresh (0–3 ppt). Current velocities in Big Beef Creek generally range from 10 to 108 $cm \cdot s^{-1}$ throughout the active channel, although backwaters with negligible flow rates are present and rising tides alter the hydrodynamic environment in the estuary (Polivka 2002). Although temperature can be greater in the estuary by as much as 1–3 °C compared with upstream, *C. aleuticus* appears to occupy areas of each habitat with equal temperatures. For example, pooled measurements at several stations in estuarine and upstream habitats taken on separate days between 15 June and 25 July 1998 give mean ± SE values of 16.11 ± 0.62 °C upstream (N = 9 days), 17.52 ± 0.30 °C in the estuary at low tide (N = 21 days), and 19.17 ± 1.2 °C in the estuary at high tide (N = 6 days). However, low-tide temperature samples taken in 2001, restricted to areas of the estuary where *C. aleuticus* occurs, were nearly identical to those taken upstream (estuary mean = 16.7 ± 0.55 °C (N = 5), upstream mean = 16.0 ± 0.25 °C (N = 10); t = 1.16, p = 0.27, df = 12). Thus, temperatures in the two major habitats differ by either a small amount or zero and are not likely to confound measures of performance in *C. aleuticus*. Salinity differences during the tide cycle can be substantial, but at least one recent study has shown that euryhaline fishes achieve optimal growth rates in brackish water (Altinok and Grizzle 2001).

Long-term census of fish and prey abundance between habitat types

I made comparisons of mean patch density across habitats by using repeated censuses of abundance. During June–August 1998–2002, I estimated the densities of *Cottus* spp. by establishing 12 semipermanent stations along the length of Big Beef Creek from the mouth of the estuary to 1.2 km upstream of the mixohaline zone generally at intervals of 50–75 m. I established six additional stations in the upper intertidal when it became clear that *C. aleuticus* was primarily found in this area and that an estuary-wide estimate of average density was inappropriate to address the question of numerical resource matching between occupied patches in both habitats. I censused all fishes once or twice per month but generally made comparisons between years by using samples from mid- to late July because comparisons for the first study year were not made until July 1998 when a consistent methodology was established. At each station, roughly standardized to an area of 6.25 m^2, field crews made two passes using a seine (2 m × 1.2 m) with a 3-mm mesh such that few individuals could avoid capture, although it is assumed that a small fraction of the cottids escaped capture underneath the seine and that any larval or extremely small juvenile individuals of all species could pass through the mesh. In general, the seining technique was identical between habitats, but the sampling frequency enabled me to determine that I was consistently seeing the same amount of variation among sites within each major habitat type as well as between habitat types. Although estuarine stations vary temporally (with the tide cycle) in depth, hydrodynamics, salinity, and temperature, censuses were always conducted at low tide in the active channel of the creek when the range of physical characteristics (including salinity) was similar for both habitats. For each species present, I recorded the standard length (SL) of each captured individual to the nearest millimetre. I compared the density of *C. aleuticus* between habitats and across years simultaneously with a two-factor analysis of variance (ANOVA). Seine censuses proved unreliable for capture of *C. asper* in upstream habitats where it appeared that they only occupied very deep pools that could not be efficiently sampled using this technique; therefore, I conducted qualitative censuses of *C. asper* abundance in upstream pools using unbaited minnow traps.

I determined the primary prey of *Cottus* in each habitat by sacrificing 10 individuals of both species with an overdose of tricaine methanesulfonate (MS 222) and identifying species found in gut samples. The primary prey items for *Cottus* in upstream habitats were stonefly larvae (*Hesperoperla* sp.) and small mayfly larvae (e.g., *Baetis* sp.), whereas primary prey items in the estuary were gammarid amphipods (*Eogammarus confervicolus* and *Corophium spinicorne*) and the marine isopod *Gnorimosphaeroma oregonense*.

I estimated the average biomass across estuarine and upstream patches of the major prey species combined by enclosing ceramic tiles (100 cm^2) in plastic mesh structures (3-mm mesh size) to allow entry and settlement by invertebrates but to prevent access and predation by fish. Ten tiles were placed in each habitat type and I allowed 2–4 weeks for invertebrates to completely settle on the tiles, which is an appropriate temporal scale for sampling populations (e.g., Peckarsky and Cowan 1995). Tiles were placed in microhabitats near the fish census stations but not directly within fish census stations to prevent disturbance of the tiles during fish censuses. Owing to the long incubation period, only one census was taken during July–August 1998, whereas in other years, there were additional censuses using tiles or other methods (Polivka 2002). For consistency, I only compared prey density between habitats and years for the July–August censuses using the ceramic tiles to correspond to comparisons of fish density. At each census, I identified all individuals to species when possible (to genus or family otherwise), obtained the total dry mass of all prey present in each sample to the nearest 0.0001 g, and compared the biomass for each habitat and year with a two-factor ANOVA. Although the major prey types in each habitat differ taxonomically, their total biomass on enclosed tiles free of fish predation might be a reasonable estimate of productivity differences between the habitats.

In analyses of both fish and prey abundance, when I found significant year effects, I performed within-habitat analysis of among-year abundance (compared with post hoc tests in a one-way ANOVA) to identify the extent of temporal varia-

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tion within each habitat independently of the other. This analysis was necessary to determine whether there was any correspondence between interannual variation in prey abundance and any interannual variation in fish abundance in either habitat.

Intraspecific competitive effects at the patch scale and resource matching at the habitat scale

If the observed densities in each major habitat type represent a resource matching equilibrium, I would expect to observe equal performance between habitats when fish are at ambient densities. Under such an equilibrium, the IFD predicts that no individual can gain fitness by moving to an alternative habitat or patch. Thus, experimental manipulation of densities and observation of performance-related response variables can identify the relative degree of saturation of major habitat types. I compared the growth of *C. aleuticus* at ambient fish densities for each habitat (calculated from census data) and at double the ambient density with in situ enclosures. If the density-dependent reduction in growth by increasing the number of estuarine fish reduces growth below that of fish at ambient density in the upstream habitat, then resources are more closely matched by fish. I also compared high-density upstream treatments and ambient density estuarine treatments, where fish density was approximately equal, thus showing the absolute difference in growth between habitats for small groups of *C. aleuticus*.

The rectangular enclosures were constructed with 3.25-mm-mesh galvanized hardware cloth and had dimensions of 61 cm × 61 cm × 31 cm. Twelve were placed in each major habitat type (estuary versus upstream) with approximately 3 cm of the respective substrate to allow incubation and colonization of prey items. Six replicates in each habitat were designated as controls (ambient density) and the other six were designated as experimental (double density) treatments. In each case, I used juvenile fish (29–35 mm initial SL) and, to simulate the densities observed in the census data obtained in each habitat, placed one or two individuals in each upstream control enclosure (ambient upstream density), two or three in estuarine controls (ambient estuarine density), two or three in upstream double-density enclosures, and four or five in estuarine double-density treatments. The range of individuals used in each treatment reflects the variation necessary to achieve a consistent total biomass per treatment that reflected ambient versus high-density conditions in each habitat. Some individuals had disappeared by the end of the experiment, and occasionally, their remains were found in the enclosures despite the rapid decomposition and consumption by scavengers (K.M. Polivka, personal observation). Whether or not remains were found, missing individuals were presumed dead and I calculated the per-enclosure survivorship for comparisons among treatments and habitats.

To identify fish for measurement of individual growth rates, I marked each fish with a small subcutaneous injection of water-based acrylic paint (Ceramcoat™) (Delta Technical Coatings, Whittier, California) at specific positions on the ventral surface of the fish and each fish received a unique color or mark position. Habitat and density effects on growth rates (in both SL and mass) were compared by a two-way ANOVA. I also estimated the Fulton condition index (CI) to test whether fish were differentially changing mass or length in response to my experimental treatments (Anderson and Neumann 1996). The index was mass × $SL^{-3.25}$ where I estimated the exponent with a regression of log(mass) versus log(SL). I used analysis of covariance to test for overall differences in mass among fish of a given length in each treatment type and to validate the CI. I tested for differences in the change in CI between habitats and density treatments with ANOVA.

Patch-scale competitive effects of *C. asper* on *C. aleuticus*

After determining the effects of conspecifics on the growth of *C. aleuticus*, I tested whether the presence of the congener *C. asper* limits the performance of *C. aleuticus* in estuarine habitats by examining the growth response among individuals at the patch scale. In 2000, I enclosed three juvenile *C. aleuticus* in 61 cm × 61 cm × 31 cm rectangular cages identical to those used previously. Although interannual differences in productivity could affect the outcome of competition, the slight, but nonsignificant, differences in estuarine fish density among years (see Results) led me to use a similar design for my experiments. In a second treatment, I again doubled the control density (six or seven *C. aleuticus*) and in a third treatment, I substituted three or four juvenile *C. asper* for the *C. aleuticus* added in the second treatment; thus, the total biomasses of fish in the second and third treatment were approximately equal. I marked each individual as before and measured the SL and mass of each fish for subsequent calculations of condition factor. Ten replicates of each treatment were placed directly in the active tidal creek channel in the estuary for 4 weeks. Enclosures were placed in a microhabitat of intermediate depth and current speed to avoid favoring one species or the other based on microhabitat associations reported in other studies (Ringstad and Narver 1973; White and Harvey 1999).

Results

Juvenile and adult *C. aleuticus* were found in both upstream habitats and the high intertidal census stations of the estuary, specifically in the upper 30% of the intertidal zone (Fig. 1*a*). Juveniles were three times more abundant than adults, numerically, in estuarine stations 8–12 (block ANOVA, $F = 13.76$, $p < 0.001$), but there was no numerical difference in adults and juveniles in upstream stations 1–12 ($F = 0.50$, $p = 0.481$). Only a few adult *C. asper* were found in a deeper pool upstream (census station 8) (Fig. 1*b*) and occasionally in minnow traps set in similar microhabitats not included in census stations. Overlap between *Cottus* spp. occurred primarily in estuarine census stations 8 and 9 but was fairly common throughout stations 8–12. In the estuary, *C. aleuticus* rarely overlapped with the primarily adult *C. asper* that occurred below station 7.

The density of *C. aleuticus* in upper estuarine stations was greater than the mean density upstream, varying from about 1.2 times greater during 1998 to nearly three times greater in 2001 (Fig. 2*a*). This pattern appears to be driven primarily by the density of juveniles in the estuary, given that adults appeared to be more frequently found upstream (Fig. 1*a*). Two way ANOVA indicated that major habitat type ($p < 0.001$) significantly explained variation in *C. aleuticus* density. Year of the study was a significant factor ($p = 0.010$)

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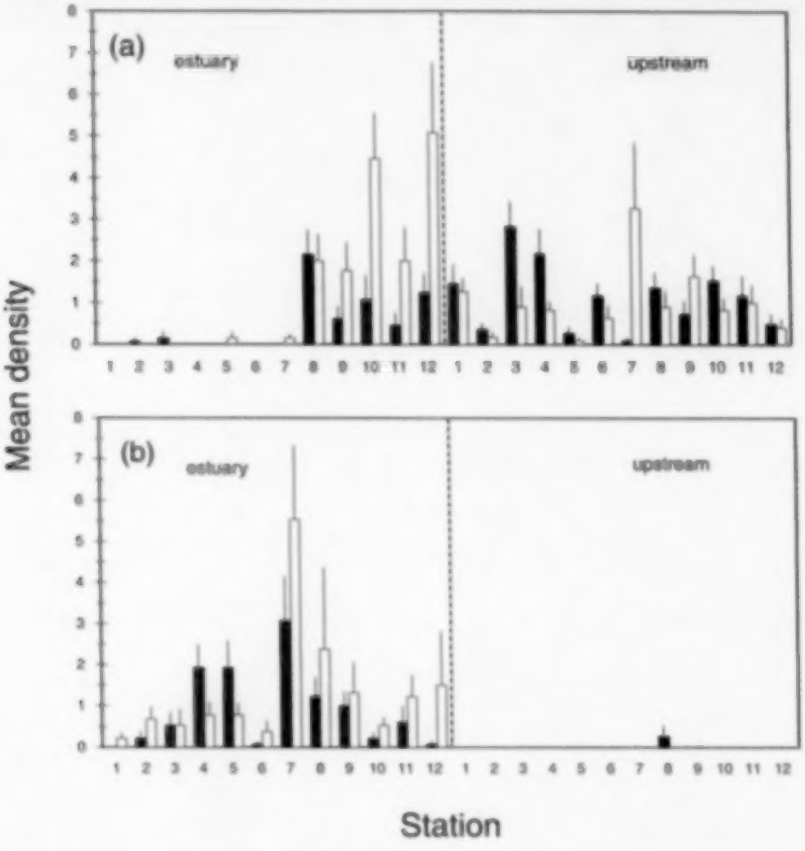
Fig. 1. Mean abundance of young-of-the-year (open bars) and adult (solid bars) individuals of (*a*) *Cottus aleuticus* and (*b*) *Cottus asper* at 12 permanent census stations in both estuarine and upstream habitats in censuses taken from 1998 to 2002 ($N = 13$ (estuary) and 11 (upstream)). Increasing station numbers indicate stations moving in an upstream direction throughout the study site.



but the interaction of these two factors was not significant ($p = 0.771$) (Table 1*a*). Upstream fish were substantially more numerous in upstream censuses (Table 1*b*) in 1998 than in 2000–2002 (Tukey's honestly significant difference (HSD) test, $p < 0.05$), whereas estuarine populations did not differ statistically among the five years of the study ($p = 0.310$) (Table 1*b*); thus, the significant year effect (Table 1*a*) is likely due primarily to the 1998 mean fish abundance.

The difference in total prey biomass between the estuary and upstream habitats varied substantially from 1.5-fold (1998) to around 40-fold (2000 and 2002), and these differences are represented by a highly significant interaction between habitat and study year ($p = 0.001$) (Table 2*a*; Fig. 2*b*). The 1998 and 1999 differences in fish and prey abundances were of similar magnitude between habitats but differed vastly from 2000 to 2002; thus, numerical matching was not consistent. One-way ANOVA indicated that differences between years in upstream prey availability were only marginally significant ($p = 0.079$) (Table 2*b*) but that estuarine prey biomass was heterogeneous among years ($p = 0.004$) (Table 2*b*). In this habitat, according to censuses taken at patches upstream of estuarine station 8, prey biomass was significantly higher ($p < 0.05$) in 2000–2002 than in 1998–1999, but within each of those groups of years, there were no significant differences (Tukey's HSD test).

Intraspecific competitive effects at the patch scale and resource matching at the habitat scale

Average individual growth rates of *C. aleuticus* stocked at ambient densities in the estuary and upstream did not indicate a resource matching equilibrium. Estuarine fish grew three times faster than those in upstream enclosures in the 1998 density manipulation experiment (Fig. 3), a result that differed slightly depending on whether the response variable examined was SL ($p = 0.053$) (Table 3a) or mass ($p = 0.003$) (Table 3*b*). Doubling the ambient density in each habitat reduced growth in mass within habitats ($p = 0.048$) but did not significantly reduce growth in SL ($p = 0.214$). Neither response variable revealed a significant interaction between habitat and density treatments, indicating that the density effect was similar in both habitats. Although growth did not show strong density dependence in the estuary, growth rates at double density are still as high as those attained at ambient density upstream. Thus, the estuary could support at least twice the observed number of individuals before growth would be equalized across both habitats in a manner

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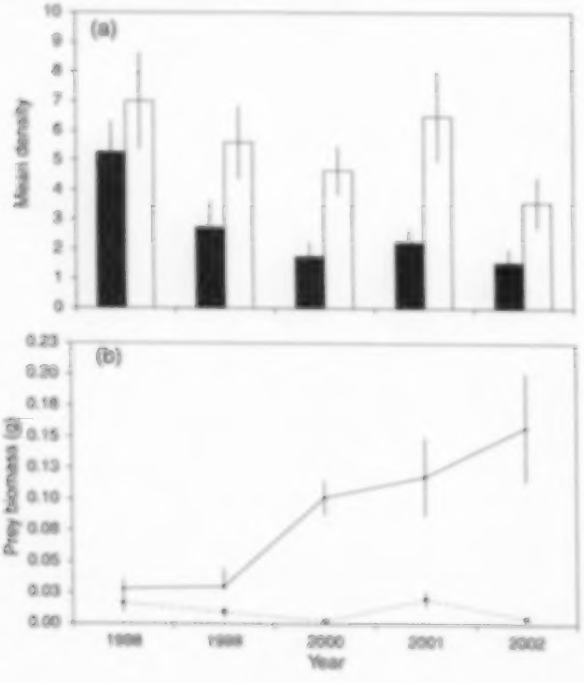
Table 1. (*a*) Two-way ANOVA of *Cottus aleuticus* density in upstream and estuarine habitats from 1998 to 2002 in each habitat and (*b*) one-way ANOVA to identify within-habitat heterogeneity in fish density among years.

Factor	df	SS	*F*	*p*
(*a*) Two-way ANOVA				
Year	4	172.01	3.47	0.010
Habitat	1	236.07	18.36	<0.001
Year × habitat	4	23.17	0.45	0.771
Error	113	1447.55		
Total	122	1878.80		
(*b*) One-way ANOVA				
Upstream				
Year	4	107.63	4.50	0.003
Error	54	323.22		
Total	58	430.85		
Estuary				
Year	4	93.4	1.23	0.310
Error	59	1124.3		
Total	63	1217.7		

Table 2. (*a*) Two-way ANOVA of prey biomass in upstream and estuarine habitats from combined census data from 1998 to 2002 in each habitat and (*b*) one-way ANOVA to identify within-habitat heterogeneity in prey biomass among years.

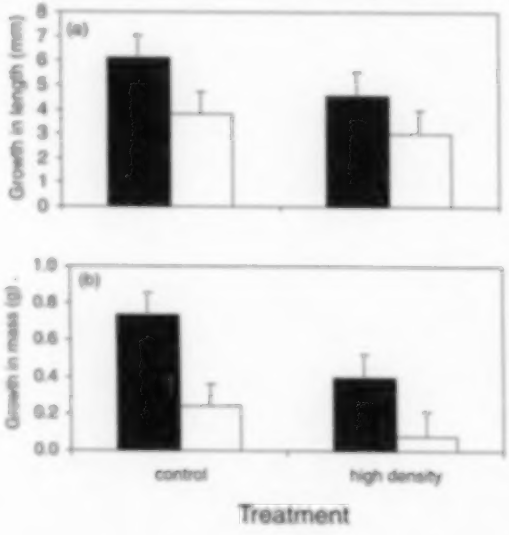
Factor	df	SS	*F*	*p*
(*a*) Two-way ANOVA				
Year	4	0.052394	4.50	0.003
Habitat	1	0.122993	45.69	<0.001
Year × habitat	4	0.055683	5.31	0.001
Error	74	0.193900		
Total	83	0.424970		
(*b*) One-way ANOVA				
Upstream				
Year	4	0.002056	2.27	0.079
Error	39	0.008823		
Total	43	0.010879		
Estuary				
Year	4	0.09676	4.57	0.004
Error	35	0.18508		
Total	39	0.28184		

Fig. 2. Mean annual abundance of (*a*) *Cottus aleuticus* and (*b*) mean annual prey biomass (mean ± SE) combined for all July–August sampling at fixed stations in estuarine versus upstream habitats for the midsummer censuses in all five years of the study (1998–2002). Solid bars, upstream fish abundance; open bars, estuary fish abundance; squares, upstream prey abundance; triangles, estuarine prey abundance.



consistent with the performance resource matching prediction of IFD-based habitat selection models. Strong productivity differences between the estuarine and upstream habitats are further indicated by the comparison between

Fig. 3. Growth measured as mean + SE change in both (*a*) standard length and (*b*) mass for replicate experimental enclosures of individual *Cottus aleuticus* maintained at ambient density (control) and twice the ambient density (high density) in both estuarine (solid bars) and upstream (open bars) habitats.



mean growth at double-density upstream and growth at ambient density in the estuary (roughly equal fish density per enclosure/patch) where growth in length was around 2.5 times greater (Fig. 3*a*) and growth in mass was around six times greater (Fig. 3*b*).

Although SL and mass both changed at different rates between habitats, the change in CI was not significantly different between habitats ($p = 0.116$), indicating that although fish grew slower upstream, they allocated growth similarly in length and mass in each habitat. The change in fish condition was 2.1 times greater at ambient densities, but this

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Table 3. Two-way ANOVA on *Cottus aleuticus* growth rates indicated by change in (*a*) standard length, (*b*) mass, and (*c*) condition index for enclosed individuals maintained at ambient and twice the ambient density in both estuarine and upstream habitats.

Factor	df	SS	*F*	*p*
(*a*) Standard length				
Habitat	1	19.922	4.280	0.053
Density	1	7.710	1.656	0.214
Habitat × density	1	0.690	0.148	0.705
Error	18	83.792		
(*b*) Mass				
Habitat	1	0.907	11.726	0.003
Density	1	0.347	4.486	0.048
Habitat × density	1	0.045	0.578	0.457
Error	18	1.392		
(*c*) Condition index				
Habitat	1	0.09680	2.72	0.116
Density	1	0.12526	3.69	0.071
Habitat × density	1	0.00401	0.12	0.735
Error	18	0.61151		
Total	21	0.83759		

effect was not significant ($p = 0.071$), nor was there a significant interaction between habitat and density ($p = 0.735$). Thus, fish condition is reduced at high densities, but a two-fold increase in estuarine density did not produce a statistically distinct effect.

Mean ± SE survivorship was similar between habitats when fish were at ambient density in each (upstream: 0.86 ± 0.09, estuary: 0.75 ± 0.17; $t = 0.58$, $p = 0.58$, df = 8), indicating no differences in average per patch survivorship due to environmental factors in each habitat including resource availability but excluding interspecific competition and predation. At high densities, survivorship was reduced (upstream: 0.75 ± 0.17, estuary: 0.59 ± 0.11; $t = 0.78$, $p = 0.46$, df = 8). Despite the downward trend in survivorship, ANOVA indicated no significant differences in survivorship between treatments ($F = 0.63$, $p = 0.605$, df = 20).

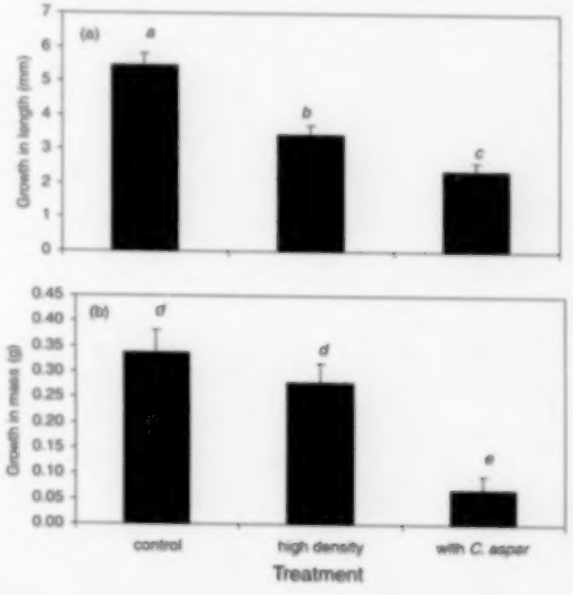
Patch-scale competitive effects of *C. asper* on *C. aleuticus*

In experimental enclosures, the presence of *C. asper* depressed the growth rate of *C. aleuticus* by a factor of more than 2, which was stronger than the intraspecific effect of doubling the density of *C. aleuticus* (Fig. 4; Table 4). Tukey's post hoc test indicated significant ($p < 0.05$) differences between all pairs of mean growth rates with the following exception: change in fish mass did not differ between the control and high-density treatments. A further consequence of interspecific competition for *C. aleuticus* is that fish condition (CI) changed by an average of –0.0817 ± 0.0217 in individuals placed with *C. asper* ($p = 0.010$) (Table 4*c*). Thus, *C. aleuticus* individuals faced with interspecific competition allocated proportionally more growth to SL than to mass, which reduced their CI from the start to the end of the experiment, whereas individuals in the ambient ($\Delta CI = -0.0021 \pm 0.0330$) and high-density ($\Delta CI = 0.0243 \pm 0.0175$) treatments added mass in equal or slightly higher proportion to SL relative to the competition treatment. Pairwise tests showed significant differences in CI between the

Table 4. Results of a one-way ANOVA on the effect of ambient densities, high densities, and the presence of *Cottus asper* on change in (*a*) standard length, (*b*) mass, and (*c*) condition index for *Cottus aleuticus* individuals.

Factor	df	SS	*F*	*p*
(*a*) Standard length				
Treatment	2	39.055	30.40	<0.001
Error	22	14.134		
Total	24	53.189		
(*b*) Mass				
Treatment	2	0.3541	16.93	<0.001
Error	22	0.2301		
Total	24	0.5842		
(*c*) Condition index				
Treatment	2	0.0552	5.77	0.010
Error	22	0.1051		
Total	24	0.1604		

Fig. 4. Change in (*a*) standard length and (*b*) mass of *Cottus aleuticus* in experimental enclosures in the estuary stocked at ambient estuarine density (control) and at twice the ambient density (high density) and in competition with *Cottus asper* (total fish biomass equal to that of the high-density treatment). Significant ($p < 0.05$) pairwise differences determined by Tukey's test are indicated by *a*–*e*.



competition treatment and both the ambient ($p = 0.029$) and high-density ($p = 0.004$) treatments but not between the ambient and high-density treatments ($p = 0.468$).

Discussion

This study considered a few of several possible mechanistic explanations for the patterns of distribution of stream fish that use estuaries opportunistically. Because estuaries are highly productive and because a limited number of species use estuaries opportunistically owing to physiological limita-

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tions, I expected to observe a strong role for resources in the habitat selection patterns of fishes and that resources might not be a limiting factor that would result in competition between ecologically similar species. Resources made the estuary profitable for fish, but resource matching was limited strongly by interspecific competition, thus preventing an equilibrium where intraspecific competitive effects would equalize fitness. Although perfect resource matching is rare in most field situations (e.g., Kennedy and Gray 1993), I initially expected to observe greater resource and fish densities in the estuary and equal growth rates across experimental patches in each habitat when these responses were measured at ambient fish densities consistent with the predictions of the IFD (Fretwell and Lucas 1970; Fretwell 1972). Despite the possibility that IFD assumptions were violated in this study system, the numerical- and performance-tracking predictions initially served as a useful null model to examine the observed spatial and temporal patterns of fish and prey abundance (e.g., Giannico and Healey 1999) and the effects of interspecific competition on the relative gains in a highly productive estuary.

Cottus aleuticus was more abundant in the estuary than in the stream, but fish abundance failed to correspond to prey abundance after a significant increase in estuarine prey biomass in 2000 was not accompanied by a similar response in mean fish density, suggesting limits to resource matching. *Cottus aleuticus* can reduce prey density at small spatial scales (K.M. Polivka, unpublished data); thus, it is surprising that a population response was not seen. The lack of a response suggests one of several possible mechanisms that limit resource matching, not all of which are addressed by the experiments in this study. These include (*i*) mechanisms at the patch scale such as predation risk and interspecific competition, (*ii*) mechanisms at the population level such as bet-hedging strategies, (*iii*) violations of resource matching assumptions, or (*iv*) a lack of active habitat selection in this species.

Because resource abundance alone could not completely explain the abundance of *C. aleuticus* in the estuarine habitat, experimental exploration of biotic interactions such as interspecific competition and predation (K.M. Polivka, unpublished data) was justified. The perceived response of fish to resource differences between habitats rests on the assumption that energetic input from the environment can support a given biomass of invertebrate consumers and a measurement of their abundance in the absence of consumption by fish is a reasonable estimate of productivity in each major habitat type. Specific studies indicating differences in energetic value of *Hesperoperla* stoneflies and *Eogammarus* amphipods are lacking and other detailed metabolic data might be necessary to demonstrate unequivocally that the total prey biomass is substitutable between habitats. Nevertheless, there is a strong indication that fish have more available prey in the estuary and that populations are limited in their ability to respond numerically to high prey availability. Additional limitations such as movement costs between the major habitat types were not the focus of this study, but there has been some indication that there are survivorship costs to movement between the stream and the estuary (K.M. Polivka, unpublished data), presumably owing to the osmoregulatory changes required in a variably saline environment, but no costs of moving from the upper intertidal zone to the lower intertidal zone (K.M. Polivka, unpublished data) where the salinity fluctuations are of greater magnitude.

Intraspecific competition had a similar effect on *C. aleuticus* in the estuarine and upstream portions of Big Beef Creek, but growth responses indicated that the estuary could support a density of *C. aleuticus* at least twice that observed in censuses before an IFD-based equilibrium would be reached. The difference in productivity between habitats might require upstream individuals to forage more widely and the artificial nature of the enclosures might limit the ability of fish to engage in normal foraging movements. However, enclosures tended to enhance the availability of upstream prey (K.M. Polivka, unpublished data), possibly owing to behavioral patterns of prey species, but not that of estuarine prey. Thus, the growth rate of upstream individuals may actually have been overestimated relative to growth rates experienced by free-ranging fish. I added a greater total number of individuals to the estuarine enclosures to double the density; thus, upstream enclosures showed the same reduction in growth with fewer additional individuals. An additional treatment where the same number of individuals were added in each habitat would be useful to examine the effects of density on growth. Density-dependent feedback mechanisms can have variable effects on a population in different habitat or patch types depending on the shape of the relationship between density and suitability (fitness) in each (Morris 1987*b*). Where density–fitness relationships can be determined directly or estimated from response variables with high correlation to fitness, isodars enable comparisons of habitat distributions when population size varies through time (Morris 1987*b*). Although population size was relatively steady in the estuary, isodars might also be useful for determining the effects of density dependence across habitats (e.g., Morris 2003) if the relationship between individual growth, survivorship, and fitness can be determined.

Interspecific competition reduced the condition of *C. aleuticus* to a greater extent than intraspecific competition. Thus, I concluded that at the microhabitat scale, *C. asper* was a superior competitor and that intraspecific competition did not limit resource matching as strongly as interspecific competition. The apparent change in growth allocation in *C. aleuticus* warrants further investigation; if *C. aleuticus* always sacrifices increases in body mass for increases in length as a result of interference competition, then there can be consequences for reproductive output via reduced gamete production (e.g., Caceres et al. 1994; Resetarits 1997) and ultimately fitness (but see Hayes and Shonkwiler 2001).

Spatial overlap in the estuarine distributions of juvenile *C. asper* and *C. aleuticus* appeared to be more frequent than has been reported for these two species in other study systems (Ringstad and Narver 1973; White and Harvey 1999). White and Harvey (1999) reported that these species were separated in streams primarily along gradients of depth and current speed, with *C. asper* occurring primarily in slower, deeper microhabitats and *C. aleuticus* occurring in shallow, fast stream riffles. Ringstad and Narver (1973) reported similar associations that extended into the mixohaline portion of a tidal creek. My upstream census data showed no overlap between these two species and *C. asper* was only found in very deep microhabitats, which is consistent with White and

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Harvey's (1999) finding, but there was considerable overlap with *C. aleuticus* in some estuarine census stations. Thus, microhabitat segregation based solely on physical properties is not sufficient to explain the coexistence of these two species in estuaries.

I conducted the competition experiments in a microhabitat that was intermediate to the reported associations of the two species in other systems (Ringstad and Narver 1973; White and Harvey 1999) and where they were known to overlap. If the reported associations with physical properties of stream microhabitats favor the dominant species in them, then I would expect the effect of *C. asper* on *C. aleuticus* to be reduced if this experiment were conducted in a shallow, fast-flowing microhabitat and possibly enhanced if it were conducted in a deep, slow-flowing pool within the estuary. In the intermediate microhabitats, *C. asper* showed a much stronger effect on the average individual growth of *C. aleuticus* than was observed in intraspecific competition treatments. Although long-term census data show that resource availability for benthic estuarine cottids was substantially higher in the year, this experiment was conducted (2000) than in the year of the density manipulation (1998), I would expect that the observed competitive effects of *C. asper* on *C. aleuticus* would be exacerbated in years of lower productivity. I did not observe strong intraspecific competition during the course of either experiment but also did not observe marked differences in the abundance of *C. aleuticus* across years where productivity differed severalfold. Patch-scale interspecific competition resulted in a strong effect of *C. asper* on the ability of *C. aleuticus* to respond to estuarine resources, which might be alleviated if microhabitat partitioning were more complete in the estuarine habitat. Competition may act synergistically with other possible mechanisms such as perceptual limitation (Abrahams 1986; Spencer et al. 1995, 1996) and other costs of habitat selection such as predation risk (Grand and Dill 1999). Nevertheless, the outcome of competition usually favors one species and similar studies have shown that competition among fish can have serious negative effects on growth and development in the weaker competitor including age-class "bottlenecks" (Persson and Greenberg 1990). My results support the further pursuit of long-term demographic consequences of competition in estuarine habitats.

Spatial and temporal variation in the use of estuaries by both fishes and invertebrates has been attributed to variable physical conditions in estuaries (Weinstein 1979; Rogers et al. 1984; Allen and Barker 1990) where temperature (Frank and Leggett 1982) and freshwater flow (Crecco and Savoy 1987) strongly influence the intraannual survival of juvenile fish that successfully enter these habitats. Species that have adapted to the physically variable estuarine environment generally benefit from high growth rates (e.g., Kneib 1984; Gray et al. 1996). Temperature varied with the influx of seawater in the estuarine system studied here, which generally affects fish growth rate (e.g., Brett 1979), but many nearshore species have wide ranges of temperature (4–6 °C) under which growth rates are optimal (e.g., Imsland et al. 1996; Jonassen et al. 1999). My in situ measurements of growth in experimental enclosures incorporated natural variation in temperature and salinity in the estuary where growth was still shown to be higher.

Population-level mechanisms may constrain the ability of estuarine-opportunist fishes such as *C. aleuticus* to match resources independently of interspecific interactions. Source–sink dynamics or bet-hedging dispersal strategies might result in a relatively consistent proportion of a population to be found in a particular habitat type. *Cottus aleuticus* juveniles were found in two habitat types that differed widely in productivity, whereas *C. asper* juveniles were exclusively found in the estuary. Disproportionate use of poor habitats is fairly common (e.g., Van Horne 1983; Grand and Dill 1997) and evolutionarily stable in some circumstances (Holt 1997; Schmidt et al. 2000; Holt and Barfield 2001); my work suggests that interspecific competition might have resulted in a habitat selection pattern for *C. aleuticus* consistent with an estuarine-opportunist strategy, but details of the broader evolutionary significance of such strategies (e.g., Pulliam 1988, 1996; Pulliam and Danielson 1991) to estuarine-opportunist species remain poorly understood. Bet-hedging by allocating a consistent proportion of individuals to estuarine or marine habitats has been proposed as a mechanism leading to anadromy in freshwater cutthroat trout (Northcote 1997), but whether this was also responsible for estuarine habitat use among the freshwater cottids in this study system is beyond the scope of the work reported here.

Deviations from the predictions of resource matching models such as the IFD may result from the forager's lack of perfect knowledge of the environment (Abrahams 1986; Kennedy and Gray 1993), which typically occurs when the spatial scale of resource heterogeneity exceeds the typical movement patterns of the forager (Tyler and Hargrove 1997) and are especially important when perceptual limits vary among individuals in a population (Spencer et al. 1996). In this study system, it is difficult to identify the extent to which individual *C. aleuticus* are able to detect differences in average resource availability across the riverine/intertidal ecotone (a violation of the "ideal" assumption of the IFD), but active habitat selection is apparent from the movement of marked individuals (K.M. Polivka, unpublished data) and differential depletion of resources on patches that vary in predation risk (K.M. Polivka, unpublished data).

Here, I showed with observational and experimental evidence that estuarine habitat selection by the euryhaline freshwater cottid *C. aleuticus* is driven in part by resources, resulting in high growth rates for a portion of the population, but limited by interspecific competition, likely contributing to underutilization of the estuary as indicated by failure to meet the predictions of simple resource matching models. Alternative models incorporate the effects of competitive differences between individuals (e.g., Hugie and Grand 1998), predation risk (e.g., Grand and Dill 1999), or local physical factors of the environment (e.g., Hill and Grossman 1993; Tyler and Gilliam 1995) on the ability of animals to match resource availability; however, relatively few of them consider the effects of interspecific competition (but see Grand 2002; Morris 2003). A forager's perceptual limits in terms of either habitat or patch-scale variation in resource availability are difficult to determine, but measurement of the effects of competition at patch scales is both tractable and valuable in resource matching studies. Identification of such costs and how they interact with other mechanisms to limit the profitability of estuaries will facilitate the evalua-

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tion of habitat selection theory and provide clues about whether and how aquatic species can respond to the variation in resources that characterize their environments.

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Practical application of meta-analysis results: avoiding the double use of data

C.V. Minte-Vera, T.A. Branch, I.J. Stewart, and M.W. Dorn

Abstract: Meta-analysis is an important new tool for synthesizing scientific knowledge from many previous studies. In fisheries, meta-analyses can be used to obtain prior distributions or penalty functions for parameters used in stock assessment models. Two types of results are generally published in a meta-analysis: Type A, the updated results for each stock used in the meta-analysis, and Type B, the results that would best describe a new stock. Including these results in assessments for the individual stocks would result in double use of the data if the assessments include the input data used in the meta-analyses, which they typically would. To solve this problem, we recommend that an additional form of results should be reported in meta-analyses: Type C, the results for a new stock obtained by sequentially excluding each stock's data set and repeating the meta-analysis. Type C results should be used whenever the assessment input data overlap with the meta-analysis input data, avoiding the double use of data. We illustrate the impact of this reporting change on the results of a recent meta-analysis.

Résumé : La méta-analyse est un nouvel outil précieux pour faire la synthèse des informations scientifiques contenues dans un grand nombre d'études antérieures. Dans le cas des pêches, les méta-analyses peuvent servir à déterminer des distributions a priori et des fonctions de pénalité pour les paramètres dans les modèles d'évaluation des stocks. On publie généralement deux types de résultats dans une méta-analyse, les premiers, de type A, les données mises à jour de chacun des stocks utilisés dans la méta-analyse et les seconds, de type B, les résultats qui décriraient le mieux un nouveau stock. Inclure ces résultats dans des évaluations de stocks individuels reviendrait à utiliser deux fois les même données, si les évaluations comprennent les données originales d'entrée de la méta-analyse, ce qui arrive normalement. Pour éviter ce problème, nous recommandons d'inclure un troisième type de résultats dans les méta-analyses, le type C, soit les résultats pour un nouveau stock en excluant tour à tour les données de chaque stock et en répétant la méta-analyse. Les résultats de type C devraient être utilisés lorsque les données d'entrée de l'évaluation chevauchent celles de la méta-analyse, ce qui permettrait d'éviter une double utilisation des données. Nous illustrons les effets de ce changement de présentation sur les résultats d'une méta-analyse récente.

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Introduction

Meta-analyses have become a powerful way of synthesizing the results of many different studies (Gurevitch and Hedges 1993; Arnqvist and Wooster 1995; Osenberg et al. 1999). Meta-analyses have been performed mainly on the results of multiple experiments (Brett and Goldman 1996; Gurevitch et al. 2000), but in applied fields of ecology, such as fisheries, time series of observations are also included. A growing number of papers have used meta-analysis to address problems that have long thwarted fisheries scientists, including the relationship between biomass and catch-per-unit-effort (Harley et al. 2001), computing survey catchabilities (Millar and Methot 2002), estimating the steepness of stock–recruitment curves (Harley and Myers 2001; Dorn 2002), and determining whether depensation occurs at small stock sizes (Myers et al. 1995; Liermann and Hilborn 1997). Meta-analyses in fisheries have been conducted using either mixed-effects models (Myers et al. 1995, 1999, 2001) or Bayesian hierarchical models (Liermann and Hilborn 1997; Harley and Myers 2001; Millar and Methot 2002). Both methods assume that there is an underlying true

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C.V. Minte-Vera,[1,2] **T.A. Branch,**[3] **and I.J. Stewart.** School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195-5020, USA.
M.W. Dorn. Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA 98115-6349, USA.

[1]Corresponding author (e-mail: cminte@u.washington.edu).
[2]Present address: Núcleo de Pesquisa em Limnologia Ictiologia e Aqüicultura, Universidade Estadual de Maringá, Maringá, PR, Brazil.
[3]Present address: Department of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch 7701, Western Cape, South Africa.

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distribution of the parameter as well as some real interstock differences, which "pull" results from individual stocks away from the average of this true distribution.

Meta-analyses hold special promise in the field of fisheries because they allow information from other stocks or species ("plausible parameter values") to be formally included in stock assessments (Hilborn and Liermann 1998). This process is most easily defined in Bayesian stock assessments, which are becoming increasingly popular (Punt and Hilborn 1997). In Bayesian models, all the parameters are assumed to be random variables with a probability distribution based on previous knowledge (a prior) that will be updated given the available data to produce a resultant probability distribution (a posterior). This process is formalized by Bayes Theorem:

$$(1) \qquad p(\boldsymbol{\theta}|\mathbf{y}) \propto p(\boldsymbol{\theta})p(\mathbf{y}|\boldsymbol{\theta})$$

The probability of the parameters ($\boldsymbol{\theta}$) given the data ($\mathbf{y}$) (the posterior) is proportional to the probability of the parameters (the prior) multiplied by the probability of the data given the parameters (the likelihood, or sampling distribution). If we assume that we know nothing at all about the parameter, then an uninformative prior is typically used (see Gelman et al. (1995) for a discussion of how to select an uninformative prior). For many parameters, such as natural mortality, depensation, and those describing stock–recruitment functions, there is often little information in a single data set. Informative priors, based on meta-analyses, are a formal way of combining information from other species or stocks for these poorly estimated parameters. Assessments based on likelihood methods can also incorporate the results of meta-analyses in the form of penalty functions that constrain the estimation process to plausible parameter values (Bard 1974). For both Bayesian and likelihood methods, the prior (or penalty function) and the data used to calculate the likelihood must be independent.

Meta-analyses are typically performed using hierarchical models. In these models, the stock-specific parameters are considered exchangeable components of a hyperdistribution, with hyperparameters assumed to be random variables (Gelman et al. 1995; Efron 1996). A hierarchical Bayesian model can be written as

$$(2) \qquad p(\boldsymbol{\theta}, \boldsymbol{\varphi}|\mathbf{y}) \propto p(\boldsymbol{\varphi})p(\boldsymbol{\theta}|\boldsymbol{\varphi})p(\mathbf{y}|\boldsymbol{\theta})$$

The joint posterior probability of the hyperparameters ($\boldsymbol{\varphi}$) and the parameters ($\boldsymbol{\theta}$) given the data ($\mathbf{y}$) is proportional to the probability of the hyperparameters (the hyperprior) multiplied by the probability of the parameters given the hyperparameters and the probability of the data given the parameters.

Standard meta-analysis outputs

We are firm believers in both meta-analysis and Bayesian stock assessments, both in the methods used and in their applications. However, we have a growing sense of unease about the manner in which all meta-analysis results are currently presented because they encourage the double use of data. Two types of results are typically presented for the parameter of interest (Fig. 1). The first is Type A, the result for each individual stock included in the meta-analysis, allowing the data for that particular stock to be "influenced" by data from the $K - 1$ other stocks (the "posterior distribution" in Bayesian meta-analysis). Following the Bayesian notation above, this distribution is

$$(3) \qquad p(\theta_i|\mathbf{y}, \boldsymbol{\varphi}, \bar{\boldsymbol{\theta}}) \propto \int_{\boldsymbol{\varphi}} \int_{\bar{\boldsymbol{\theta}}} p(\boldsymbol{\theta}, \boldsymbol{\varphi}|\mathbf{y}) \mathrm{d}\bar{\boldsymbol{\theta}}\, \mathrm{d}\boldsymbol{\varphi}$$

The marginal posterior probability distribution for the stock i given the data ($\mathbf{y}$), the parameters of the other stocks excluding stock i ($\bar{\boldsymbol{\theta}}$), and the hyperparameters ($\boldsymbol{\varphi}$) is proportional to the integral of the joint posterior distribution. These results should be used for further work on one of the stocks in the meta-analysis, provided that none of the data in the meta-analysis will be included. The second is Type B, the result for an "unobserved stock" (a synthesis of the data from all the stocks in the meta-analysis, the "posterior predictive distribution" in Bayesian meta-analysis). In Bayesian terms, the distribution of the parameters for an unobserved stock (θ_{K+1}) given the information from the K observed stock is

$$(4) \qquad p(\theta_{K+1}|\mathbf{y}) \propto \int_{\boldsymbol{\varphi}} \int_{\boldsymbol{\theta}} p(\theta_{K+1}|\boldsymbol{\varphi})p(\boldsymbol{\theta}, \boldsymbol{\varphi}|\mathbf{y}) \mathrm{d}\boldsymbol{\theta}\, \mathrm{d}\boldsymbol{\varphi}$$

This distribution can answer questions about the evidence for a particular hypothesis as well as the effect size of a given parameter. Type B results should be used as assessment inputs for stocks that were not included in the meta-analysis.

In standard Bayesian analyses, informative priors are obtained using knowledge available before the new experiment commences (Gelman et al. 1995). The collected data are then used to update the priors and obtain posteriors. In contrast, stock assessments are not independent discrete experiments but are based on time series data. Stock assessments usually incorporate many sources of data, including survey indices, yearly total catches, proportions of fish of each age, and commercial catch-per-unit-effort indices. These data sources are simultaneously fit to model predictions based on assumed underlying population dynamics equations (see, for example, Methot 1990). Those model predictions include stock biomasses and recruitment used as inputs in fisheries meta-analyses (e.g., Myers et al. 1999; Dorn 2002). Because these time series of data are increased each year by one or more data points, past data are nearly always retained as part of the updated assessment. For this reason, any informative prior based on past knowledge, i.e., on meta-analyses that use any of the input data used in past stock assessments, is going to include data that are still used in the current assessment. This double use of data will generally result in a posterior distribution for the parameter that is biased and has an incorrect associated level of uncertainty (Gelman et al. 1995, p. 122). Both Type A and Type B results are afflicted by this double use of data if they are used as informative priors (in Bayesian analyses) or as penalty functions (in likelihood analyses) in future analyses.

Solution for the double use of data

We suggest that to discourage the inadvertent double use of data and to broaden the applicability of meta-analytical results, authors should also report a third form of results in their papers (Fig. 2): Type C, the result for an "unobserved stock" obtained by excluding the stock being assessed from the meta-analysis. This could also be called an "independent

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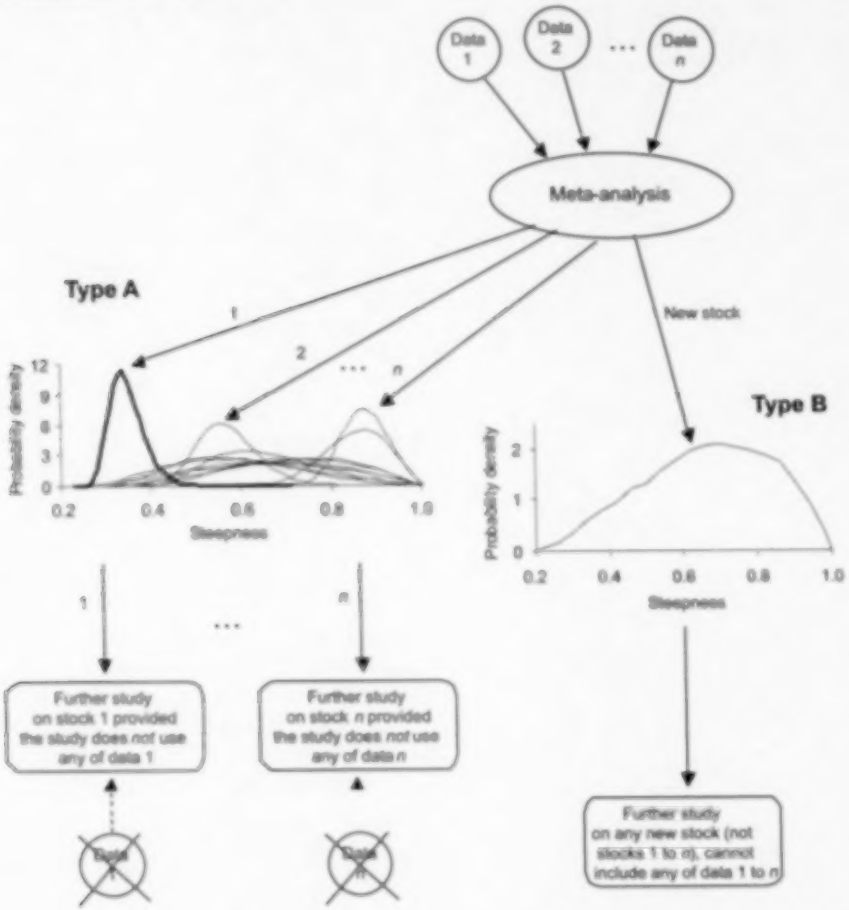
Fig. 1. Standard reporting of results from meta-analysis showing the flow from input data to the meta-analysis, to Type A and Type B results from the meta-analysis, and finally to future studies or stock assessments that incorporate Type A and Type B results. The distributions for steepness are those obtained from the meta-analysis conducted by Dorn (2002). Under Type A, stock 1 (in bold) is the west coast Pacific ocean perch (*Sebastes alutus*) stock.


Data 1
Data 2
Data n
Meta-analysis
Type A
1
2
n
New stock
Type B
Probability density
Steepness
Further study on stock 1 provided the study does not use any of data 1
Further study on stock n provided the study does not use any of data n
Further study on any new stock (not stocks 1 to n), cannot include any of data 1 to n

predictive posterior" in Bayesian meta-analysis. A separate Type C result will be required for each of the stocks included in the meta-analysis. These results should be used whenever the same input data are used for both the meta-analysis and the subsequent application, avoiding the double use of data.

Illustration

We illustrate our point by examining the recently published Bayesian meta-analysis on the steepness of rockfish stock–recruitment relationships (Dorn 2002) with the aim of producing results appropriate for use in an updated US west coast Pacific ocean perch (*Sebastes alutus*) stock assessment. Steepness is the fraction of preexploitation recruitment produced when spawning biomass is at 20% of preexploitation levels (Fig. 3). Dorn's (2002) meta-analysis produced posterior distributions for steepness based on fitting a hierarchical model to spawning biomass and recruitment time series generated by previous stock assessments. This framework allowed sharing of information between stocks, strengthening the inference for those stocks with short time series (Dorn 2002). However, because the biomass and recruitment series were assessment model predictions, they were based on time series data that could not be discarded in future assessments. In the case of west coast Pacific ocean perch, when producing an updated assessment model, only a few years of additional data would be added to the 40-year time series used in the meta-analysis. The Type A estimate of steepness (Beverton–Holt model) for the west coast Pacific ocean perch stock had a mean of 0.35 (SD = 0.039) and a relatively narrow distribution. The Type B estimate of steepness for an unobserved stock had a mean of 0.66 (SD = 0.17). The estimate of steepness for west coast Pacific ocean perch was markedly lower than estimates for the other stocks (Dorn 2002), and therefore, the Type B estimate was influenced in two ways: the overall mean was decreased and the estimated variability among stocks was increased. However, neither the Type A nor the Type B results should be included in the stock assessment for west coast Pacific ocean perch because of the double use of data. The process leading to double use of data is outlined in Fig. 1, where data from west coast Pacific ocean perch (stock 1) flow into

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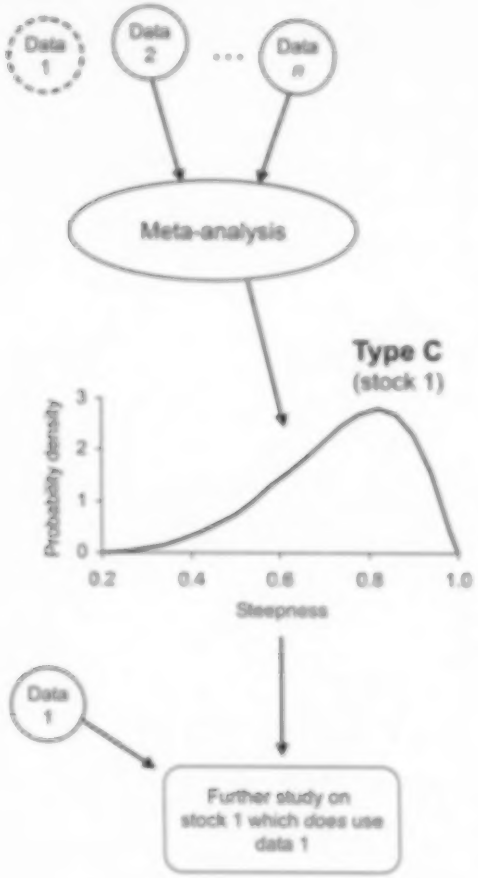
Fig. 2. Proposed additional reporting of results from meta-analysis showing how data from stock 1 (west coast Pacific ocean perch (*Sebastes alutus*) in this example) need to be excluded from the meta-analysis to obtain Type C results for this stock. We reran the meta-analysis of Dorn (2002) omitting data for west coast Pacific ocean perch to obtain the illustrated Type C curve. Note that future stock assessments can use the Type C posterior from the meta-analysis distribution as a prior on steepness in the assessment and still include the data for this stock without double use of data.



the meta-analysis and are incorporated into the Type A and Type B results. Future assessments that include Type A or Type B results and the data used in the meta-analysis will be therefore be guilty of double use of data.

To produce results appropriate for use in an updated stock assessment, we therefore reran the analysis in Dorn (2002), excluding the west coast Pacific ocean perch data, to obtain the Type C distribution of steepness (as illustrated in Fig. 2). The Type C distribution has a higher mean of 0.74 and less uncertainty (SD = 0.14) than the Type B distribution (mean = 0.66, SD = 0.17). This Type C distribution (the independent predictive posterior for the meta-analysis) can be safely used as the prior in a Bayesian stock assessment. We compared the effect of using the incorrect Type B distribution and the correct Type C distribution as priors for steepness in the current stock assessment model for west coast Pacific ocean

Fig. 3. Illustration of the steepness parameter for two stock–recruitment functions with steepness values of 0.8 (broken curve) and 0.4 (solid curve). Steepness is the fraction of preexploitation recruitment produced when spawning biomass is at 20% of preexploitation levels.

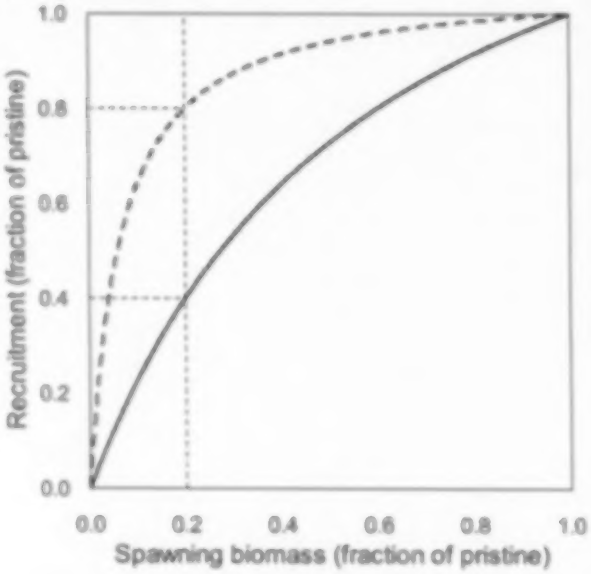
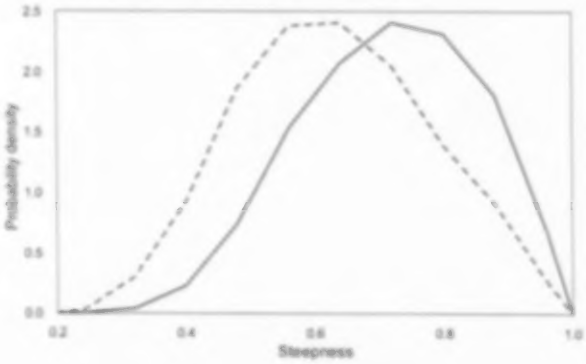


Fig. 4. Posterior distributions for steepness obtained from a stock assessment of west coast Pacific ocean perch (*Sebastes alutus*) that either incorrectly used the Type B distribution (broken line) or correctly used the Type C distribution (solid line) as a prior on steepness. The meta-analysis distributions (Types B and C) were incorporated as informative priors into the current assessment model for this stock, and updated posterior distributions for steepness were obtained from the assessment.



perch (Ianelli 2002). These priors were then updated using the assessment model, producing posteriors for steepness that were markedly different for the Type B prior (mean = 0.63, SD = 0.15) versus the Type C prior (mean 0.72, SD = 0.14) (Fig. 4). This difference in the posterior distribution for steepness from the assessment model does not result in a large change in the mean estimate of current depletion (which increases from mean = 0.30, SD = 0.10 to mean = 0.33, SD = 0.10) but will translate into substantial differ-

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ences in future recruitment predictions. For example, median predicted recruitment (1 year into the future) when using the Type B prior is 7.2% higher than when using the Type C prior. This difference would increase if predictions were made farther into the future, as higher predicted recruitments will be followed by larger spawning biomass, which in turn will produce higher subsequent recruitments.

Discussion

The approach we recommend will entail an additional burden in both analysis time and reporting space. It may be possible to show through simulation that, for a large number of data sets, there is little effect of removing the single stock of interest. However this "contamination" of the prior with the data would still be incorrect. Because the fish stocks used in meta-analyses are generally those with better data, and those for which assessments are done on a regular basis (i.e., the most commercially important), these are the very stocks most likely to be assessed with the informative priors created. Therefore, it is imperative that reported meta-analysis results be practically applicable to all future studies and assessments. Current reporting methods require stock assessment scientists to contact the authors of meta-analyses to request that they rerun their analyses to obtain proper Type C results.

In summary, we suggest that in order for scientists to use the results of meta-analysis correctly, analysts should report all three types of results stated above. It is then up to the users to employ Type A results if their stock was included in the meta-analysis but they are not reusing any of the data that were used in the meta-analysis, Type B results if their stock was not included in the meta-analysis, and Type C results if their model shares any of the data that were used in the meta-analysis. The development and use of Type C results may also provide an additional benefit as a tool for comparing the information content of data sets used in meta-analysis.

In this paper, we have focused on the problems of applying meta-analyses to fisheries stock assessments (our specialty). However, we are well aware that this issue, and our proposed solution, are applicable to any scientific field that presents or uses the results of meta-analyses based on time series data, like ecological risk assessments and climate modeling.

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Escapement, harvest, and unknown loss of radio-tagged adult salmonids in the Columbia River – Snake River hydrosystem

Matthew L. Keefer, Christopher A. Peery, William R. Daigle, Michael A. Jepson, Steven R. Lee, Charles T. Boggs, Kenneth R. Tolotti, and Brian J. Burke

Abstract: Accurate estimates of escapement by adult anadromous salmonids are difficult, especially in large, multistock river systems. We used radiotelemetry and a fishery reward program to calculate escapement, harvest, and unaccounted for loss rates for 10 498 adult chinook salmon (*Oncorhynchus tshawytscha*) and 5324 steelhead (*Oncorhynchus mykiss*) during six return years in the Columbia River basin. Mean annual escapements to spawning sites, hatcheries, or the upper bounds of the monitored hydrosystem were 73.4% (spring–summer chinook salmon), 61.3% (fall chinook salmon), and 62.6% (steelhead). Mean reported harvest rates were 8.7% (spring–summer chinook), 22.0% (fall chinook), and 15.1% (steelhead) within the mainstem hydrosystem and 5.9%, 3.4%, and 5.7%, respectively, in lower hydrosystem tributaries. On average, 12%–17% of each run had unknown fates in the mainstem hydrosystem. Escapement, harvest, and loss varied significantly between runs and years, within runs between known-origin subbasin stocks, and between interdam river reaches. Multiyear quantitative assessments like this can reduce uncertainty, clarify inter- and intra-annual variability, and help managers better evaluate fisheries, identify conservation priorities, and help protect evolutionarily significant populations.

Résumé : Il est difficile d'estimer avec précision les échappements des salmonidés adultes, particulièrement dans les grands réseaux hydrographiques qui contiennent plusieurs stocks. Nous avons utilisé la radiotélémétrie et un programme de pêche avec récompenses pour calculer l'échappement, les captures et les taux de pertes inexpliquées pour 10 498 saumons quinnat adultes (*Oncorhynchus tshawytscha*) et 5324 truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) durant six années de montaison dans le bassin hydrographique du fleuve Columbia. Les échappements annuels moyens vers les sites de fraie, les pisciculture et les limites supérieures du système hydrographique sous surveillance sont de 73,4 % (saumons quinnat de printemps et d'été), 61,3 % (saumons quinnat d'automne) et 62,6 % (truites arc-en-ciel anadromes). Les taux moyens de captures signalées sont de 8,7 % (saumons quinnat de printemps et d'été), 22,0 % (saumons quinnat d'automne) et 15,1 % (truites arc-en-ciel anadromes) dans le cours principal et respectivement de 5,9, 3,4 et 5,7 % dans les tributaires du cours inférieur. En moyenne, le sort de 12–17 % des poissons de chaque montaison reste inconnu dans le cours principal. L'échappement, la capture et la perte varient significativement d'une montaison à une autre et d'une année à l'autre; ils varient aussi au sein d'une même montaison parmi les stocks identifiés comme provenant de divers sous-bassins, de même que dans les divers tronçons de rivière entre les barrages. Des estimations comme les nôtres qui couvrent plusieurs années peuvent réduire l'incertitude, préciser la variation annuelle et inter-annuelle et aider les gestionnaires à mieux évaluer les pêches, fixer les objectifs prioritaires de conservation et protéger les populations d'importance évolutive.

[Traduit par la Rédaction]

Introduction

The Columbia River and its largest tributary, the Snake River, were historically among the most productive anadromous salmonid *Oncorhynchus* spp. river systems in the world (Chapman 1986; Nemeth and Kiefer 1999), with predevelopment annual runs estimated at between 10 and 16 million adult fish (Northwest Power Planning Council 1986). A combination of habitat loss, water diversion, hatchery propagation, excessive harvest, and development of the federal hydrosystem decimated many of the runs (National Research Council 1996; McClure et al. 2003). Numerous

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M.L. Keefer,[1] **C.A. Peery, W.R. Daigle, M.A. Jepson, S.R. Lee, C.T. Boggs, and K.R. Tolotti.** Idaho Cooperative Fish and Wildlife Research Unit, Biological Resources Division, US Geological Survey, University of Idaho, Moscow, ID 83844-1141, USA.
B.J. Burke. Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, Seattle, WA 98112-2097, USA.

[1]Corresponding author (e-mail: mkeefer@uidaho.edu).

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Columbia basin stocks are extinct (Nehlsen et al. 1991), and 12 salmon and steelhead (*Oncorhynchus mykiss*) populations are currently listed as threatened or endangered under the US Endangered Species Act (National Marine Fisheries Service 2000).

Ensuring adequate adult escapement to natal spawning grounds is critical for managing extant stocks and for re-establishing suppressed or locally extinct populations. Fish counts, performed on returning adult migrants while passing hydroelectric dams of the Columbia and Snake rivers, are good relative indicators of annual aggregated run size, but spawning escapement has remained difficult to accurately measure (Dauble and Mueller 1993, 2000). Several factors confound escapement estimates, including counting errors, uncertainties associated with commercial, tribal, sport, and illegal fisheries, problems quantifying interdam tributary turnoff, undetected mainstem spawning, temporary or permanent interbasin straying, and fish fallback and reascension at dams. Given the federal mandate to protect US Endangered Species Act listed runs, clarification of these and other uncertainties identified in the biological opinion on operation of the Federal Columbia River hydrosystem (National Marine Fisheries Service 2000) are among the priorities for agencies involved in the Columbia River salmon and steelhead recovery process (National Research Council 1996; Independent Scientific Advisory Board 2001).

Radiotelemetry has been a useful tool for determining passage timing (Keefer et al. 2004*b*), spatial distribution and movement patterns (Wuttig and Evenson 2001), and ultimate fates of large numbers of individually marked migratory salmonids (Skalski et al. 2001; McPherson et al. 2003). Mobile and fixed radiotelemetry arrays can passively monitor tagged fish at sites where access is difficult or traditional sampling methods are unrealistic (Eiler 1990, 1995). High transmitter return rates can be achieved through fishery reward programs and cooperative agreements with management agencies (e.g., Keefer et al. 2004*c*). Telemetry methods are particularly effective in river systems where upstream migrants pass through constricted areas like fish ladders at hydroelectric dams (Gerlier and Roche 1998; Gowans et al. 1999) or when fish disperse over wide, but accessible, geographic areas (Milligan et al. 1985; Bjornn et al. 2003).

In response to concerns of the US Army Corps of Engineers, National Oceanic and Atmospheric Administration (NOAA) Fisheries, and state and tribal agencies regarding recovery of anadromous fish runs of the Columbia and Snake rivers, we radio-tagged and monitored almost 16 000 adult chinook salmon (*Oncorhynchus tshawytscha*) and steelhead from 1996 to 2002. All fish were collected at Bonneville Dam, the first hydroelectric project fish encounter after leaving the Pacific Ocean. Our objectives were to examine upstream passage behavior, distribution to tributaries and hatcheries, and escapement through the federal hydrosystem. In this paper, we present estimates of dam-to-dam and hydrosystem-wide escapement along with reach-specific harvest and loss rates for chinook salmon and steelhead runs and for selected subbasin populations. We also examine the influence of seasonal river discharge and temperature and the effects of fallback, an influential fish behavior (Boggs et al. 2004), on annual escapement estimates.

Methods

Fish trapping, tagging, and monitoring

Adult steelhead and spring, summer, and fall chinook salmon were trapped at Bonneville Dam (river kilometre 235) in the adult fish facility adjacent to the Washington-shore fish ladder as they migrated upstream in the Columbia River (Fig. 1). Each day that fish were tagged, a weir was lowered into the ladder to divert fish into the adult fish facility via a short secondary ladder. Once inside the facility, fish were either diverted into anesthetic tanks for tagging or returned to the main ladder without handling.

During six study years, radio transmitters were placed in a total of 15 822 adult fish from the three largest Columbia River runs: 6290 spring–summer chinook salmon (April–July, six years), 4208 fall chinook salmon (August–October, four years), and 5324 steelhead (June–October, five years) (Table 1). On average, radio-tagged samples represented 0.78% of spring–summer chinook salmon, 0.40% of fall chinook salmon, and 0.26% of steelhead counted passing Bonneville Dam each year (US Army Corps of Engineers 2002). Columbia River basin hatcheries fin-clipped some, but not all, juveniles released that contributed to adult runs in 1996–2002. Mean proportions of fin-clipped fish in the radio-tagged samples were 45% (spring–summer chinook), 11% (fall chinook), and 74% (steelhead). Fish were tagged throughout each run in approximate proportion to long-term average counts at Bonneville Dam; variability in daily counts and annual run timing precluded precise proportional sampling. Owing to high water temperatures, no summer chinook were tagged in July 1996 and no fall chinook were tagged in August 1998.

Protocols for fish trapping, handling, intragastric insertion of radio transmitters, and fish recovery were the same in all years and are described in Keefer et al. (2004*c*). As much as possible, spring–summer chinook salmon and steelhead were nonselectively tagged as they were trapped from 1996 to 1998. Samples were not truly random because only fish passing via the Washington-shore ladder were sampled, proportions sampled each day varied, and no fish were sampled at night. To accommodate transmitter sizes (see Keefer et al. (2004*c*) for transmitter types and dimensions), we also did not tag jack (precocious adult) salmon or steelhead with fork length <50 cm. Among fall chinook salmon, we selected for upriver-bright fish, a group that spawns mostly in the Hanford Reach of the Columbia River, the Snake River, or the Deschutes River, and limited our collection of sexually mature Tule fall chinook salmon that return only a short distance upstream to Bonneville reservoir hatcheries (Myers et al. 1998).

In 2000–2002, tagging methods were modified to include use of an automated system (McCutcheon et al. 1994) that identified fish with passive integrated transponder (PIT) tags as they passed through the adult fish facility trap. PIT tags indicated if and where fish were tagged as juveniles (referred to here as known-source fish because their natal sites were known), and use of PIT-tagged fish allowed us to make stock-specific harvest, escapement, and unaccounted for loss estimates. We attempted to radio-tag as many known-source fish as possible within the 2000–2002 tagging schedules.

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Fig. 1. Columbia and Snake rivers showing dams monitored with radiotelemetry (inset map shows the location of the study region in the northwestern United States). For this study, the hydrosystem was bounded by Bonneville, Lower Granite, and Priest Rapids dams. Other monitored dams include The Dalles (TD), John Day (JD), McNary (MN), Ice Harbor (IH), Lower Monumental (LM), and Little Goose (GO). Major Columbia River tributaries within the studied hydrosystem that were monitored with radio antennas: 1, Wind; 2, Little White Salmon; 3, White Salmon; 4, Hood; 5, Klickitat; 6, Deschutes; 7, John Day; 8, Umatilla; 9, Walla Walla; 10, Snake; 11, Yakima.

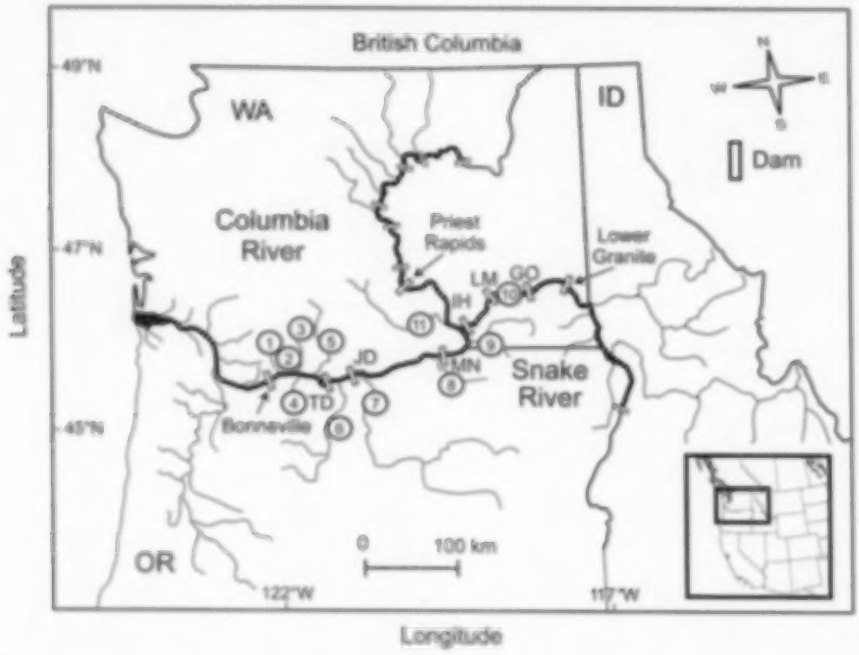

Table 1. Number of adult chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) tagged with radio transmitters at Bonneville Dam from 1996 to 2002 that were released downstream from the dam or into the dam forebay.

	1996	1997	1998	2000	2001	2002	Total
Released downstream from Bonneville Dam							
Spring–summer chinook	853	1014	957	973	829	900	5 526
Fall chinook	—	—	1032	745	561	756	3 094
Steelhead	765	975	—	843	804	945	4 332
Released into Bonneville Dam forebay							
Spring–summer chinook	—	—	—	159	288	317	764
Fall chinook	—	—	—	373	431	310	1 114
Steelhead	—	—	—	317	347	328	992
Total	1618	1989	1989	3410	3260	3556	15 822

Note: 25 fish (0.16%) were not released with transmitters for various reasons.

Known-source fish were radio-tagged as they were trapped, and fish without PIT tags made up the remainder of each daily sample. The proportions of radio-tagged fish that had been PIT-tagged as juveniles in 2000, 2001, and 2002 were 6%, 70%, and 37% (spring–summer chinook), <1%, 13%, and 6% (fall chinook), and <1%, 61%, and 46% (steelhead), respectively (Table 2). To differentiate from known-source groups, unselectively collected fish without juvenile PIT tags are referred to as unknown-source in this paper. Fish PIT-tagged as juveniles at lower Columbia River dams were included in the unknown-source group because their natal sites were unknown. Similarly, very small samples ($n < 5$ per site) of known-source fish from lower Columbia tributaries were included in the unknown-source group. Treatment of the latter group did not affect results.

Several secondary markers were used to help identify fish that lost transmitters during the study period. From 1996 to 1998, each radio-tagged fish had a coded wire tag injected into the dorsal sinus and a unique alphanumeric visible implant tag inserted into the clear tissue posterior to one eye. Visible implant tags were also used in 2000, and a new PIT tag was inserted into the abdominal cavity of most fish that

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Table 2. Number of radio-tagged adult chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) of known origin as identified by passive integrated transponder (PIT) tags implanted when fish were juveniles.

	Downstream releases			Forebay releases		
	2000	2001	2002	2000	2001	2002
Spring–summer chinook						
Wind River[a]	—	17	35	—	12	14
John Day River	—	—	13	—	—	2
Snake River	28	348	168	—	125	19
Yakima River	—	92	66	—	28	32
Upper Columbia River[b]	37	105	73	—	37	26
Other[c]	1	8	1	—	7	2
Fall chinook						
Snake River	5	26	36	2	36	3
Other[c]	2	35	16	1	33	4
Steelhead						
Snake River	6	239	370	1	123	66
Upper Columbia River[b]	2	186	84	—	141	56
Other[c]	—	11	6	—	2	5

Note: Groups with samples <10 were not used in statistical tests and were included in the unknown-source category. See Fig. 1 for source locations.

[a]All fish PIT-tagged at Carson National Fish Hatchery.

[b]Upstream from Priest Rapids Dam.

[c]Fish in the "Other" category were tagged at multiple sites, primarily lower Columbia dams and tributaries, and were included in the unknown-source samples.

had not been PIT-tagged as juveniles. In 2001 and 2002, PIT tags (original or newly inserted) were used exclusively as secondary markers.

After tagging and recovery from anesthesia, all radio-tagged fish in 1996–1998 were released about 9.5 km downstream from Bonneville Dam at sites on both sides of the Columbia River. From 2000 to 2002, 74%–86% of spring–summer chinook salmon, 57%–71% of fall chinook salmon, and 70%–74% of steelhead were released at the downstream sites and the rest were released into the Bonneville Dam forebay, just upstream from the face of the dam. Forebay releases were used to evaluate dam operations (spillway and powerhouse allocation) and specific fish behaviors related to fishway exit sites (Reischel and Bjornn 2003). Downstream release locations were the same in all years, so we primarily present results for fish released at those sites. To reduce bias related to radio-tagging, including permanent downstream movement or mortality (e.g., Bernard et al. 1999), we excluded downstream-released fish that did not reascend fishways at Bonneville Dam from analyses. Data from forebay-released fish were treated separately and were principally used to validate results when samples were adequate.

Radio-tagged fish were monitored with an extensive array of aerial and underwater antennas at dams and tributaries of the Columbia and Snake rivers (Fig. 1). Passage was continuously monitored at the four lower Columbia River dams and at Priest Rapids Dam on the upper Columbia River in all years and at the four lower Snake River dams in all years except 1996, when only Ice Harbor and Lower Granite dams were monitored. Fixed aerial antennas were installed in all major Columbia River tributaries between Bonneville and Priest Rapids dams except the Umatilla River in 1996. Additional tributaries downstream from Bonneville Dam had aerial antennas in 1996 and 1998. Aerial antennas were also in primary and secondary Snake River tributaries upstream from Lower Granite Dam in all years except 1996 (only the Clearwater River was monitored in 1996). Data from fixed aerial and underwater antennas were supplemented with data collected while surveying segments of the basin from boats or trucks mounted with receivers and aerial antennas. More complete descriptions of antenna types and locations are included in Bjornn et al. (2000) and Keefer et al. (2004*a*, 2004*b*).

Fish fate and escapement estimation

Final fish distributions were assessed from the combination of telemetry records from fixed sites, mobile tracking efforts in tributaries and reservoirs, and transmitter returns from hatcheries, fish traps, and spawning ground surveys conducted by cooperating agencies. Transmitters were also returned from commercial, sport, and tribal fisheries through a reward program. Standard reward values printed on all transmitters were US$25 but ranged from US$10 to US$100. PIT tag detectors installed in fishways at Lower Granite and McNary dams provided additional passage data in the later years of the study for fish that may have regurgitated transmitters. This extra monitoring had a negligible effect on fate determination for chinook salmon but changed fate designations for 1%–3% of steelhead from 2000 to 2002. From the above data sources, fates for radio-tagged fish were arranged into six basic categories: fish either (*i*) passed the upstream extent of the study area for this analysis (Lower Granite or Priest Rapids Dam), (*ii*) were reported harvested in a mainstem fishery, (*iii*) entered a tributary (or the Hanford Reach spawning grounds for fall chinook salmon), (*iv*) were reported harvested in a tributary fishery, (*v*) entered

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Table 3. Notation used in escapement calculations.

Entered reach i	E_i	
Passed reach[a]	P	
Escapement 1	$Esc_1 = (P + T_i + T_d + H_i + H_d) \cdot (E_i)^{-1}$	
Escapement 2	$Esc_2 = (P + T_i + T_d + H_i + H_d + TF_i + TF_d) \cdot (E_i)^{-1}$	
Escapement 3	$Esc_3 = (P + T_i + T_d + H_i + H_d + TF_i + TF_d + MF_i + MF_d) \cdot (E_i)^{-1}$	
	Fish was last recorded:	
	Within reach i	Downstream from reach i
Mainstem fishery	MF_i	MF_d
Tributary	T_i	T_d
Tributary fishery	TF_i	TF_d
Hatchery or trap	H_i	H_d
Unknown fate	U_i	U_d

[a]Subsequent downstream movement ignored.

a hatchery or trap, or (*vi*) had unknown fate (Table 3). Possible dispositions of fish with unknown fate included mortality, illegal or unreported harvest, lost transmitters, and undetected hydrosystem exit. Fish that passed Lower Granite or Priest Rapids dams were considered to have escaped the monitored hydrosystem regardless of subsequent downstream movement.

Fate summaries were used to estimate escapement values for the entire hydrosystem and for specific river segments containing an individual dam and reservoir complex (dam-to-dam reach) for each species and run year and for subsets of the tagged fish based on release site, release dates, and known-source groups. Individual reaches were bounded by the tops of dam fishways. For example, the Bonneville – The Dalles reach started when fish exited the top of a Bonneville Dam fishway (or were released into the Bonneville Dam forebay) and ended with an exit from a fishway at The Dalles Dam. In this study, the hydrosystem was bounded by the tops of Bonneville Dam, Lower Granite Dam (the most upstream Snake River dam with fish passage), and Priest Rapids Dam (the most upstream Columbia River dam monitored in all years).

Managers use escapement indices for multiple purposes and within different jurisdictions (e.g., for tributary versus mainstem fisheries), so we elected to calculate three estimates with progressively less stringent criteria for defining successful escapement. Escapement 1 (Esc_1) was the most basic and most stringent measure, where all fish harvested from mainstem or tributary sites (downstream from Lower Granite and Priest Rapids dams) and all fish with unknown fates did not escape (Table 3). Esc_1 was an inappropriate measure for between-group comparisons because stocks originating upstream from Lower Granite or Priest Rapids dams had limited exposure to tributary fisheries downstream from these dams and we did not include harvest upstream from those sites. Escapement 2 (Esc_2) treated fish harvested in hydrosystem tributaries as successful, but mainstem-harvested fish as unsuccessful, and was therefore a measure of total escapement to tributaries or the upper bounds of the monitored hydrosystem. Escapement 3 (Esc_3) treated all harvested fish as successful (i.e., mortality was not associated with hydrosystem operations), and only fish with unknown fates within the hydrosystem were considered unsuccessful. Esc_3 eliminated variability associated with harvest and was therefore a good measure of underlying between-year, between-run, and between-stock differences in escapement. Esc_3 also approximated potential escapement through the monitored hydrosystem in the absence of fisheries. In all estimates, fish that passed the upstream end of a reach or the hydrosystem were considered to have escaped, regardless of subsequent downstream movement.

We calculated 95% profile likelihood confidence intervals (Lebreton et al. 1992) for each estimate using the mark–recapture software program MARK (White and Burnham 1999). Profile likelihood intervals are asymmetric and appropriate when parameters, like escapement, are bounded by (0,1) (Lebreton et al. 1992). The program MARK was also used to compare escapement estimates (Esc_2 and Esc_3 only) for groups of tagged fish, again focusing on downstream-released fish. Null models that assumed constant escapement within a run year or across multiple years were compared with models that assumed variable escapement through time. Likelihood ratio tests were used to evaluate competing models (White and Burnham 1999) along with χ^2 tests to quantify statistical differences between fish groups (e.g., based on juvenile PIT tag site, adult release location, or adult release timing). The addition of PIT tag detectors at Lower Granite and McNary dams resulted in some changed fish fate designations in later years, so between-year and between-group statistical comparisons of escapement were based on telemetry and recapture data only (PIT data ignored) to reduce bias associated with changes in methodology.

River environment and fallback analyses

Linear regression was used to examine relationships between river environment variables and annual escapement and harvest estimates for the unknown-source groups. Independent variables were annual mean and maximum discharge and temperature collected at Bonneville Dam (http://www.cqs.washington.edu/dart/dart.html) during the date range that each run passed the dam. Run dates for chinook salmon followed those established by US Army Corps of Engineers (2002): April–July for spring–summer chinook salmon and August–October for fall chinook salmon. Environmental data from June–October were used for steelhead, as the majority of this protracted run passes Bonneville Dam

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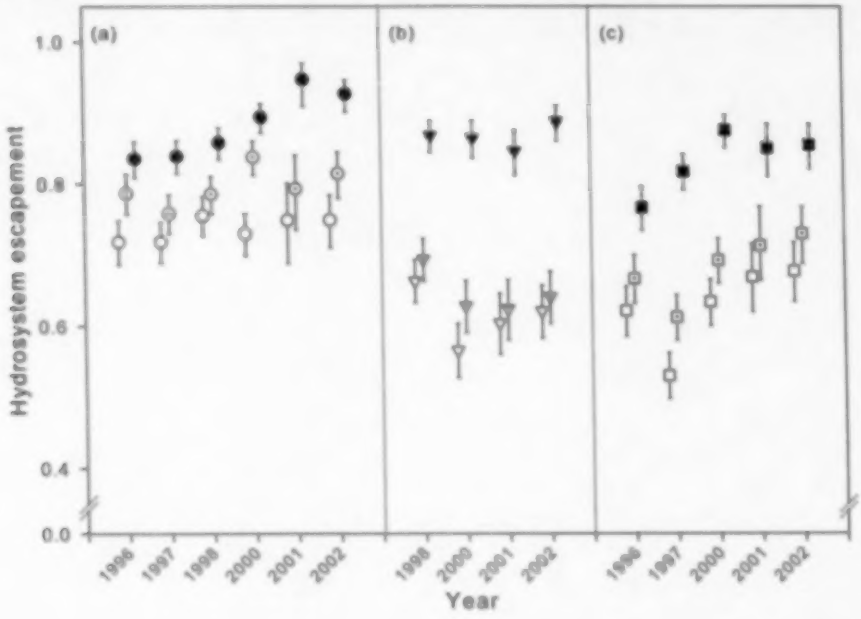
Fig. 2. Annual hydrosystem (Bonneville Dam to Lower Granite or Priest Rapids dams) escapement estimates for unknown-source radio-tagged (*a*) spring–summer chinook salmon (*Oncorhynchus tshawytscha*), (*b*) fall chinook salmon, and (*c*) steelhead (*Oncorhynchus mykiss*) released downstream from Bonneville Dam. Open symbols, Escapement 1 (Esc_1); dotted symbols, Escapement 2 (Esc_2); solid symbols, Escapement 3 (Esc_3). Error bars are 95% profile likelihood confidence intervals.



during that period. As with other between-year tests, only telemetry and recapture data were included in escapement estimates.

Many adult salmon and steelhead pass Columbia River hydrosystem dams and then fall back downstream (Boggs et al. 2004), sometimes resulting in lower escapement (Bjornn et al. 2000). We compared Esc_3 estimates, which eliminated variability associated with harvest, for fish that either did or did not fallback within both known- and unknown-source groups using Pearson's χ^2 tests. The potential cumulative impact of fallback on hydrosystem escapement for each population was calculated by multiplying escapement differences by the proportion of each run (or known-source group) recorded falling back during migration.

Results

Hydrosystem escapement estimates

Unknown-source fish

Mean hydrosystem Esc_1 estimates for all unknown-source fish released downstream from Bonneville Dam were 0.734 (SD = 0.015) for spring–summer chinook salmon, 0.614 (0.035) for fall chinook salmon, and 0.626 (0.052) for steelhead (Fig. 2). Reported mainstem harvest downstream from Lower Granite and Priest Rapids dams ranged from 5% to 25% of each run, with mean rates of 8.7% (spring–summer chinook), 22.0% (fall chinook), and 15.1% (steelhead) (Table 4). Reported harvest in hydrosystem tributaries ranged from 2% to 10% of each run, with means of 5.9% for spring–summer chinook, 3.4% for fall chinook, and 5.7% for steelhead. Fish with unknown fates made up 5%–16% (mean = 11.6%) of spring–summer chinook, 11%–15% (13.3%) of fall chinook, and 12%–23% (16.7%) of steelhead released at the downstream sites.

Means for Esc_2, which treated fish harvested in tributaries as escaped, were 0.792 (SD = 0.026) for spring–summer chinook salmon, 0.647 (0.028) for fall chinook salmon, and 0.683 (0.041) for steelhead. Means for Esc_3, which treated all fish harvested anywhere downstream from Lower Granite or Priest Rapids dams as successful, were 0.875 (SD = 0.042) for spring–summer chinook, 0.867 (0.014) for fall chinook, and 0.834 (0.038) for steelhead.

In all within-year comparisons of Esc_2, spring–summer chinook salmon escaped at higher rates (χ^2 tests, $0.0000 < P < 0.014$) than both fall chinook salmon and steelhead, and steelhead escaped at higher rates than fall chinook salmon ($0.022 \leq P \leq 0.051$) (Fig. 2). Esc_3 estimates differed significantly in 5 of 12 within-year comparisons: spring–summer chinook salmon escaped at higher rates than steelhead in 1996, 2001, and 2002 ($P < 0.001$) and at higher rates than fall chinook salmon in 2001 ($P = 0.0001$) and 2002 ($P = 0.024$).

Adult escapement was not constant between years for the three runs (Fig. 2). Interannual variation in Esc_2 estimates was significant for spring–summer chinook salmon (likelihood ratio test, $\chi^2 = 20.21$, df = 5, $P = 0.001$), fall chinook salmon ($\chi^2 = 10.46$, df = 3, $P = 0.015$), and steelhead ($\chi^2 = 16.50$, df = 4, $P = 0.002$). Significant interannual differences were also found in Esc_3 estimates for spring–summer chinook salmon ($\chi^2 = 53.84$, df = 5, $P < 0.0001$) and steelhead

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Table 4. Number of radio-tagged fish used in each estimate (E_i) and the percentage (n in parentheses) of the total in each fate category with hydrosystem escapement estimates for all fish released downstream from Bonneville Dam or in the Bonneville Dam forebay for unknown-source stocks and for known-source stocks identified by passive integrated transponder (PIT) tags, 1996–2002.

Year	Release	Stock	E_i	P	T_{ind}*	H_{ind}	TF_{ind}	MF_{ind}	U_{ind}	Esc_1	Esc_2	Esc_3
Spring–summer chinook salmon (*Oncorhynchus tshawytscha*)												
1996	Downstream	Unknown	810	28 (228)	27 (219)	17 (135)	7 (55)	5 (40)	16 (133)	0.719	0.786	0.836
1997	Downstream	Unknown	952	52 (499)	10 (95)	9 (90)	4 (38)	8 (77)	16 (153)	0.719	0.758	0.839
1998	Downstream	Unknown	932	46 (432)	16 (152)	13 (120)	3 (28)	7 (68)	14 (132)	0.755	0.785	0.858
2000	Downstream	Unknown	888	45 (396)	14 (126)	14 (126)	11 (96)	6 (50)	11 (94)	0.730	0.838	0.894
2001	Downstream	Unknown	227	59 (135)	10 (22)	6 (13)	4 (10)	15 (35)	5 (12)	0.749	0.793	0.947
2002	Downstream	Unknown	534	54 (286)	11 (61)	10 (52)	7 (36)	11 (60)	7 (39)	0.747	0.815	0.927
2000	Forebay	Unknown	157	53 (83)	15 (23)	10 (15)	5 (8)	5 (8)	13 (20)	0.772	0.823	0.873
2001	Forebay	Unknown	124	54 (67)	7 (9)	9 (11)	6 (8)	11 (14)	12 (15)	0.702	0.766	0.879
2002	Forebay	Unknown	226	50 (112)	14 (32)	10 (23)	5 (12)	11 (24)	10 (23)	0.739	0.792	0.898
2001	Downstream	Wind River	16	—	—	31 (5)	44 (7)	6 (1)	19 (3)	0.313	0.750	0.813
2002	Downstream	Wind River	35	—	31 (11)	17 (6)	26 (9)	20 (7)	6 (2)	0.486	0.743	0.943
2001	Forebay	Wind River	12	—	17 (2)	42 (5)	25 (3)	8 (1)	8 (1)	0.500	0.833	0.917
2002	Forebay	Wind River	13	—	15 (2)	38 (5)	31 (4)	15 (2)	—	0.538	0.846	1.000
2002	Downstream	John Day River	12	—	83 (10)	—	8 (1)	—	8 (1)	0.833	0.917	0.917
2000	Downstream	Snake River	27	78 (21)	—	—	—	—	22 (6)	0.778	0.778	0.778
2001	Downstream	Snake River	338	82 (277)	2 (6)	<1 (1)	1 (2)	11 (36)	5 (16)	0.840	0.846	0.953
2002	Downstream	Snake River	165	78 (128)	1 (2)	—	—	12 (19)	10 (16)	0.788	0.788	0.903
2001	Forebay	Snake River	124	78 (97)	—	1 (1)	1 (1)	17 (21)	3 (4)	0.790	0.798	0.968
2002	Forebay	Snake River	19	95 (18)	—	—	—	—	5 (1)	0.947	0.947	0.947
2001	Downstream	Yakima River	92	—	20 (18)	59 (54)	11 (10)	2 (2)	9 (8)	0.783	0.891	0.913
2002	Downstream	Yakima River	65	—	74 (48)	3 (2)	11 (7)	9 (6)	3 (2)	0.769	0.877	0.969
2001	Forebay	Yakima River	28	—	14 (4)	71 (20)	11 (3)	4 (1)	—	0.857	0.964	1.000
2002	Forebay	Yakima River	32	—	75 (24)	3 (1)	9 (3)	9 (3)	3 (1)	0.781	0.875	0.969
2000	Downstream	Upper Columbia River	37	86 (32)	3 (1)	—	—	3 (1)	8 (3)	0.892	0.892	0.919
2001	Downstream	Upper Columbia River	105	86 (90)	1 (1)	—	—	3 (3)	10 (11)	0.867	0.867	0.895
2002	Downstream	Upper Columbia River	73	86 (63)	—	—	—	4 (3)	10 (7)	0.863	0.863	0.904
2001	Forebay	Upper Columbia River	35	74 (26)	—	—	—	6 (2)	20 (7)	0.743	0.743	0.800
2002	Forebay	Upper Columbia River	26	85 (21)	—	—	—	4 (1)	12 (4)	0.808	0.808	0.846
Fall chinook salmon												
1998	Downstream	Unknown	913	3 (28)	48 (434)	16 (144)	3 (28)	17 (159)	13 (120)	0.664	0.694	0.869
2000	Downstream	Unknown	659	11 (73)	39 (258)	6 (42)	6 (41)	24 (156)	14 (89)	0.566	0.628	0.865
2001	Downstream	Unknown	495	9 (46)	39 (191)	12 (61)	2 (11)	22 (110)	15 (76)	0.602	0.624	0.847
2002	Downstream	Unknown	644	9 (59)	46 (296)	7 (45)	2 (13)	25 (159)	11 (72)	0.621	0.641	0.888
2000	Forebay	Unknown	371	6 (23)	37 (136)	6 (24)	3 (11)	37 (136)	11 (41)	0.493	0.523	0.890
2001	Forebay	Unknown	395	10 (40)	38 (149)	11 (44)	2 (7)	22 (88)	17 (67)	0.590	0.608	0.830
2002	Forebay	Unknown	307	13 (39)	39 (117)	7 (20)	3 (10)	22 (67)	18 (54)	0.573	0.606	0.824
2001	Downstream	Snake River	26	77 (20)	4 (1)	—	—	12 (3)	7 (2)	0.808	0.808	0.923
2002	Downstream	Snake River	34	59 (20)	—	—	—	24 (8)	18 (6)	0.588	0.588	0.824
2001	Forebay	Snake River	36	72 (26)	—	—	—	3 (1)	25 (9)	0.722	0.722	0.750

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Table 4 (*concluded*).

Year	Release	Stock	E_i	P	T_{ind}[a]	H_{ind}	TF_{ind}	MF_{ind}	U_{ind}	Esc_1	Esc_2	Esc_3
Steelhead (*Oncorhynchus mykiss*)												
1996	Downstream	Unknown	724	40 (290)	19 (134)	4 (26)	5 (33)	10 (72)	23 (169)	0.622	0.667	0.767
1997	Downstream	Unknown	916	37 (342)	12 (110)	4 (34)	8 (75)	21 (188)	18 (167)	0.531	0.612	0.818
2000	Downstream	Unknown	814	46 (372)	14 (118)	3 (26)	6 (48)	18 (149)	12 (101)	0.634	0.693	0.876
2001	Downstream	Unknown	363	51 (187)	12 (43)	4 (13)	4 (16)	14 (50)	15 (54)	0.669	0.714	0.851
2002	Downstream	Unknown	478	49 (234)	17 (82)	2 (8)	5 (25)	13 (60)	14 (69)	0.678	0.730	0.856
2000	Forebay	Unknown	315	42 (132)	10 (33)	2 (6)	6 (18)	24 (76)	16 (50)	0.543	0.600	0.841
2001	Forebay	Unknown	83	48 (40)	17 (14)	5 (4)	1 (1)	11 (9)	18 (15)	0.700	0.711	0.819
2002	Forebay	Unknown	205	53 (108)	12 (25)	1 (2)	7 (15)	10 (20)	17 (35)	0.659	0.732	0.829
2001	Downstream	Snake River	234	71 (166)	7 (16)	—	2 (4)	10 (23)	11 (25)	0.778	0.812	0.893
2002	Downstream	Snake River	359	76 (274)	4 (13)	—	1 (2)	11 (39)	9 (31)	0.799	0.805	0.914
2001	Forebay	Snake River	122	82 (100)	3 (4)	—	1 (1)	7 (8)	7 (9)	0.852	0.861	0.926
2002	Forebay	Snake River	66	71 (47)	8 (5)	—	—	9 (6)	12 (8)	0.788	0.788	0.879
2001	Downstream	Upper Columbia River	183	75 (138)	4 (7)	—	3 (5)	9 (16)	9 (17)	0.792	0.820	0.907
2002	Downstream	Upper Columbia River	82	77 (63)	4 (3)	—	6 (5)	10 (8)	4 (3)	0.805	0.877	0.963
2001	Forebay	Upper Columbia River	141	62 (88)	2 (3)	—	4 (5)	20 (28)	12 (17)	0.645	0.681	0.879
2002	Forebay	Upper Columbia River	56	66 (37)	—	—	5 (3)	20 (11)	9 (5)	0.661	0.714	0.911

Note: The hydrosystem includes the top of Bonneville Dam to the top of Lower Granite or Priest Rapids dams. Data includes corrections from PIT-tag-only detections at dams. See Table 3 for fate categories.

[a]Tributary category includes Hanford Reach spawning areas for fall chinook salmon.

(χ^2 = 36.49, df = 4, P < 0.0001) but not for fall chinook salmon (χ^2 = 4.37, df = 3, P = 0.224).

Within individual run years (Fig. 3), Esc_2 estimates varied significantly over 2-week intervals (likelihood ratio tests, $P \leq 0.006$) in four of six spring–summer chinook salmon runs (1996, 1997, 2000, and 2002), all four fall chinook salmon runs ($P \leq 0.006$), and two of five steelhead runs (1996 and 2002) ($P < 0.011$). Differences in Esc_3 estimates were significant ($P < 0.03$) within two spring–summer chinook salmon runs (1996 and 2002), two fall chinook salmon runs (2000 and 2002), and two steelhead runs (2000 and 2002).

Hydrosystem escapement estimates for unknown-source fish released downstream were compared with those for fish released in the forebay in 2000, 2001, and 2002. Of the 27 pairs (3 runs × 3 years × 3 escapement estimates), 6 (22%) differed significantly (χ^2 tests, $P \leq 0.05$). Forebay-released fish had lower escapement by 6.8%–10.5% (mean = 8.6%) in all six significant pairs, which included spring–summer chinook salmon in 2001 (Esc_3), fall chinook salmon in 2000 (Esc_1 and Esc_2) and 2002 (Esc_3), and steelhead in 2000 (Esc_1 and Esc_2) (Table 4). Nonsignificant pairs differed by <0.1% to 4.2% (mean = 2.3%).

Known-source fish

Stock-specific hydrosystem escapements were calculated for known-source fish from the Wind, John Day, Yakima, Snake, and upper Columbia rivers (Table 4). Large proportions of downstream-released spring–summer chinook salmon from Wind River were reported harvested in 2001 and 2002, mostly in the Wind River itself (44% and 26%) but also in the Columbia River mainstem (6% and 20%). Escapement estimates for Wind River fish ranged from 0.313 (Esc_1 in 2001) to 0.943 (Esc_3 in 2002) (Fig. 4). Less than 1% of Snake River spring–summer chinook salmon were reported harvested in tributaries downstream from Lower Granite Dam (fish were temporary or permanent strays) and a total of 10.4% (range = 0%–12%) were reported harvested in mainstem fisheries (Table 4). Mean escapements for Snake River spring–summer chinook salmon were 0.802 (Esc_1), 0.804 (Esc_2), and 0.878 (Esc_3) for the three years (Fig. 4). Yakima River spring–summer chinook salmon were harvested in the Yakima River (11% in both 2001 and 2002) and Columbia River (2% and 9%) and escapements ranged from 0.769 (Esc_1) to 0.969 (Esc_3). There was minimal harvest of upper Columbia River spring–summer chinook salmon and all escapement estimates were between 0.863 and 0.919. Escapement estimates for forebay-released fish from each of these stocks did not differ (χ^2 tests, $P \geq 0.09$) from those for downstream-released fish.

No downstream-released Snake River fall chinook salmon were reported recaptured in tributaries downstream from Lower Granite Dam, but 12% (2001) and 24% (2002) were harvested in mainstem fisheries. Escapement estimates were 0.808 (2001) and 0.588 (2002) for both Esc_1 and Esc_2 and were 0.923 (2001) and 0.833 (2002) for Esc_3 (Fig. 4). Differences between downstream- and forebay-released fish were not significant ($P > 0.05$).

Nine to 11% of downstream-released Snake River and upper Columbia River steelhead stocks were reported harvested in mainstem fisheries and another 2%–6% were reported harvested in tributaries downstream from Lower Granite and

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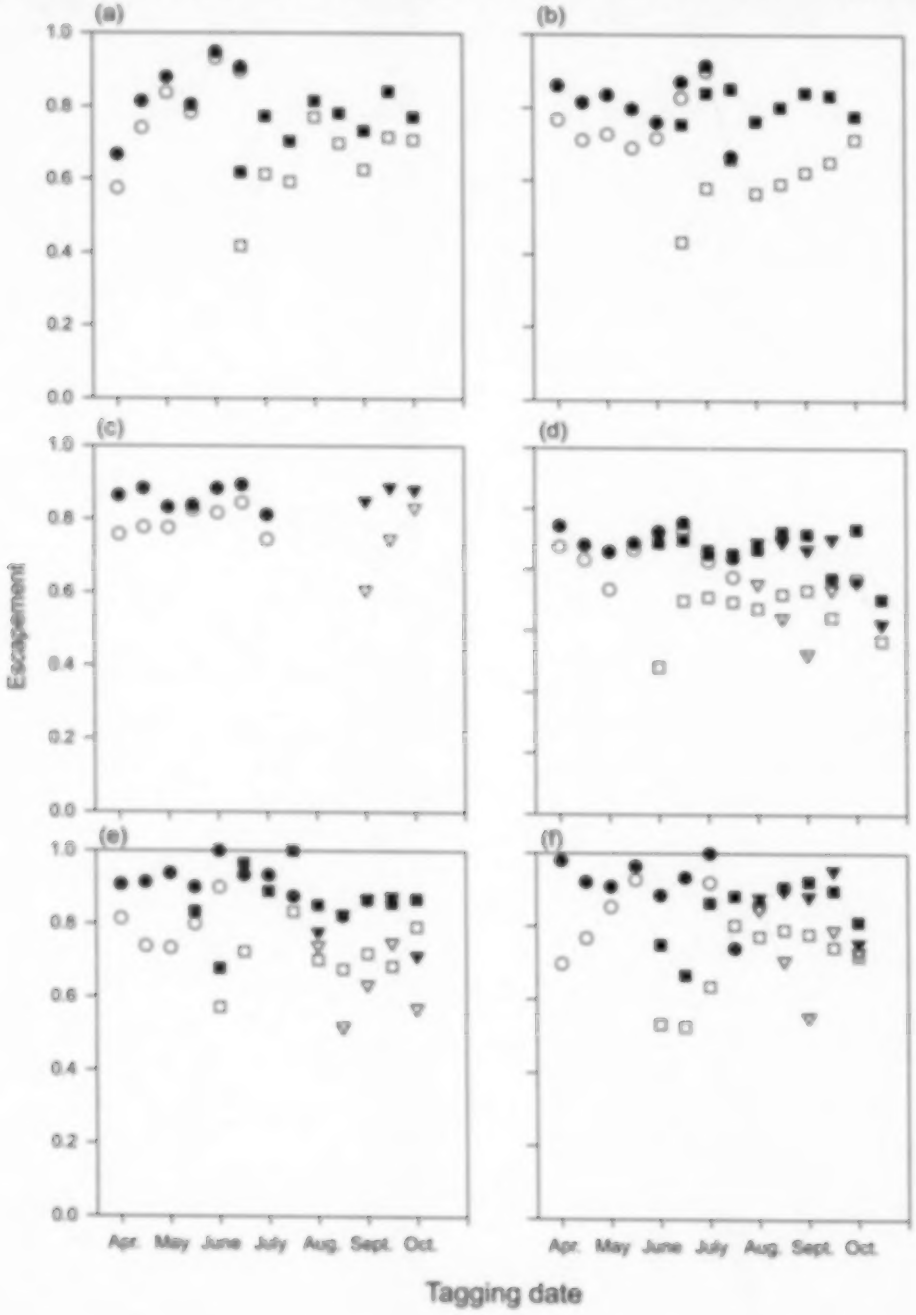
Fig. 3. Biweekly hydrosystem Escapement 2 (Esc_2) (open symbols) and Escapement 3 (Esc_3) (solid symbols) estimates for radio-tagged spring–summer chinook salmon (*Oncorhynchus tshawytscha*) (circles), fall chinook salmon (triangles), and steelhead (*Oncorhynchus mykiss*) (squares) released downstream from Bonneville Dam. (*a*) 1996; (*b*) 1997; (*c*) 1998; (*d*) 2000; (*e*) 2001; (*f*) 2002.



Priest Rapids dams (fish were temporary or permanent strays). Notably, 20% of forebay-released upper Columbia River steelhead were harvested in mainstem fisheries. Snake River and upper Columbia River steelhead escapements were between 0.778 (Esc_1) and 0.963 (Esc_3) (Fig. 4). Forebay-released upper Columbia River steelhead escaped at lower rates ($0.003 < P < 0.056$, Esc_1 and Esc_2) than downstream-released upper Columbia River fish in 2001 and 2002. Escapements did not differ between release sites for Snake River steelhead.

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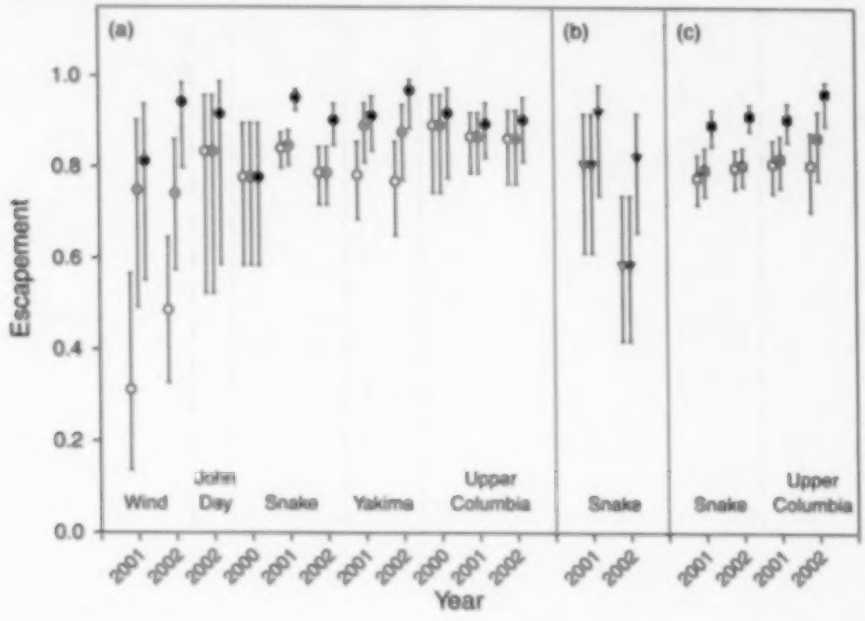
Fig. 4. Annual hydrosystem (Bonneville Dam to Lower Granite or Priest Rapids dams) escapement estimates for known-source radio-tagged (*a*) spring–summer chinook salmon (*Oncorhynchus tshawytscha*), (*b*) fall chinook salmon, and (*c*) steelhead (*Oncorhynchus mykiss*) released downstream from Bonneville Dam. Open symbols, Escapement 1 (Esc_1); dotted symbols, Escapement 2 (Esc_2); solid symbols, Escapement 3 (Esc_3). Error bars are 95% profile likelihood confidence intervals.



Among-group comparisons

Among spring–summer chinook salmon, no differences (χ^2 tests, $P > 0.05$) were found in Esc_2 or Esc_3 estimates for the three groups available for comparison in 2000 (unknown source, Snake, and upper Columbia) or the six in 2002 (unknown source, Wind, John Day, Snake, Yakima, and upper Columbia) (Figs. 2 and 4). Five groups were compared in 2001 (unknown source, Wind, Snake, Yakima, and upper Columbia): Esc_3 was higher for Snake River fish (0.953) than for upper Columbia River (0.895) and Wind River (0.813) fish ($0.01 < P < 0.04$). Esc_3 was also higher for the unknown-source group (0.947) than for Wind River fish ($P = 0.031$) in 2001, and Esc_2 was higher for Yakima River fish (0.891) than for the unknown-source group (0.793) ($P = 0.038$).

No escapement differences ($P > 0.05$) were found between Snake River fall chinook salmon and unknown-source fall chinook salmon in 2001 or 2002. Upper Columbia River steelhead escaped at higher rates than Snake River and unknown-source steelhead. Esc_2 estimates were higher ($0.002 < P < 0.045$) for upper Columbia River fish in 2001 and 2002, and Esc_3 estimates were higher ($0.007 < P < 0.034$) in 2002.

Within individual known-source stocks, no between-year Esc_2 differences were significant ($P > 0.05$) for spring–summer chinook salmon (Snake, upper Columbia, Yakima, and Wind), fall chinook salmon (Snake), or steelhead (Snake and upper Columbia). Esc_3 was significantly higher for Snake River spring–summer chinook salmon in 2001 (0.953) than in 2000 (0.778) (χ^2 tests, $P = 0.002$) and 2002 (0.903, $P = 0.032$). No other within-stock Esc_3 comparisons differed between years ($P > 0.05$).

There was less statistically significant within-run year escapement variance for known-source stocks than for unknown-source groups, in part because sample sizes for each interval were small. Only Snake River spring–summer chinook salmon in 2001 (Esc_2) and upper Columbia River steelhead in 2001 (Esc_3) showed significant (likelihood ratio tests, $P < 0.05$) within-run variance. Late-migrating spring–summer chinook salmon and early-migrating steelhead had lower escapement in those runs.

Treatment of interbasin strays may have positively biased escapement estimates. Between 1.5% and 2.0% of spring–summer and fall chinook salmon and about 6% of steelhead from stocks of the Snake, Yakima, and upper Columbia rivers were last recorded in lower Columbia River tributaries. Most strays entered tributaries to the Bonneville reservoir or the Deschutes River or John Day River, and about one third were harvested and may have been temporary strays only. By definition, fish that entered these tributaries were considered escaped (Esc_2 and Esc_3) regardless of ultimate destination. Escapement estimates for known-source groups would be lower by approximately the above percentages if strays were treated as unsuccessful migrants.

Reach-specific escapement estimates

Unknown-source fish

Individual reach escapements were lowest for all runs between Bonneville and The Dalles dams in the lower Columbia River and were relatively high through all lower Snake River reaches (Fig. 5). Mean Esc_1 estimates for downstream-released fish in the Bonneville – The Dalles reach were

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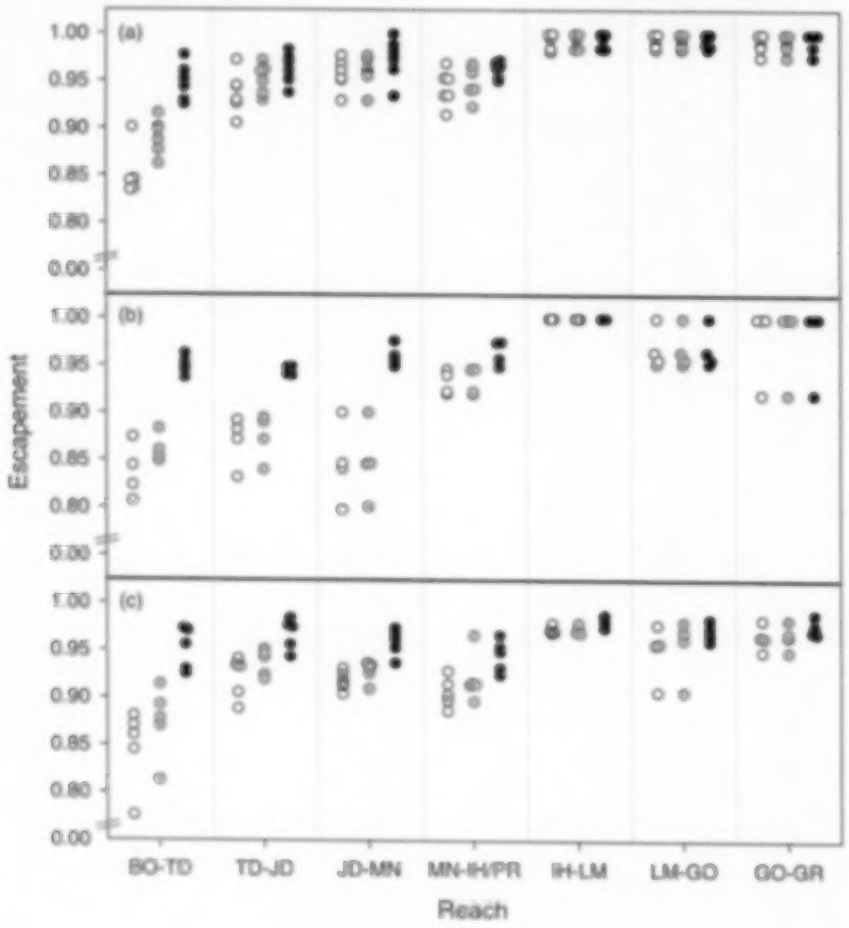
Fig. 5. Annual (1996–2002) reach-specific escapement estimates for unknown-source radio-tagged (*a*) spring–summer chinook salmon (*Oncorhynchus tshawytscha*), (*b*) fall chinook salmon, and (*c*) steelhead (*Oncorhynchus mykiss*) released downstream from Bonneville Dam. Abbreviations for dams are as follows: BO, Bonneville; TD, The Dalles; JD, John Day; MN, McNary; IH, Ice Harbor; PR, Priest Rapids; LM, Lower Monumental; GO, Little Goose; GR, Lower Granite. Open symbols, Escapement 1 (Esc_1); dotted symbols, Escapement 2 (Esc_2); solid symbols, Escapement 3 (Esc_3).



0.850 for spring–summer chinook salmon, 0.837 for fall chinook salmon, and 0.847 for steelhead. Esc_1 means for spring–summer chinook salmon were between 0.937 and 0.957 through the other three lower Columbia River reaches and were ≥0.991 through the three Snake River reaches. Esc_1 means for fall chinook salmon and steelhead were between 0.847 and 0.933 through The Dalles – John Day, John Day – McNary, and McNary – Ice Harbor/Priest Rapids reaches. Esc_1 means in lower Snake River reaches were higher for fall chinook salmon (0.968–1.000) than for steelhead (0.960–0.978) (Fig. 5).

Less than 7% of downstream-released fish that entered each reach were subsequently reported harvested in tributaries ($(TF_i + TF_d)(E_i)^{-1}$) (Fig. 6) (see Table 3 for notation). Most tributary harvest for spring–summer chinook salmon occurred in the Wind River (39% of all tributary harvest), Deschutes River (21%), and Little White Salmon River (19%). Tributary harvest of fall chinook salmon was primarily in the Klickitat River (71%). Most steelhead were harvested in the Deschutes River (25%), Klickitat River (19%), Little White Salmon River (15%), and John Day River (13%). The distribution of tributary harvest resulted in little difference between mean Esc_1 and Esc_2 values in most reaches except Esc_2 means were slightly higher for the Bonneville – The Dalles and The Dalles – John Day reaches (Fig. 5).

As many as 15% of downstream-released fish that entered each reach were subsequently harvested in the mainstem Columbia or Snake rivers ($(MF_i + MF_d)(E_i)^{-1}$) (Fig. 6). Mainstem harvest rates were highest for fish entering the Bonneville – The Dalles reach for spring–summer chinook salmon (mean = 5.8%) and steelhead (7.7%) and in the John Day – McNary reach (11.1%) for fall chinook salmon. Fall chinook salmon were also harvested at relatively high rates after entering the Bonneville – The Dalles (mean =

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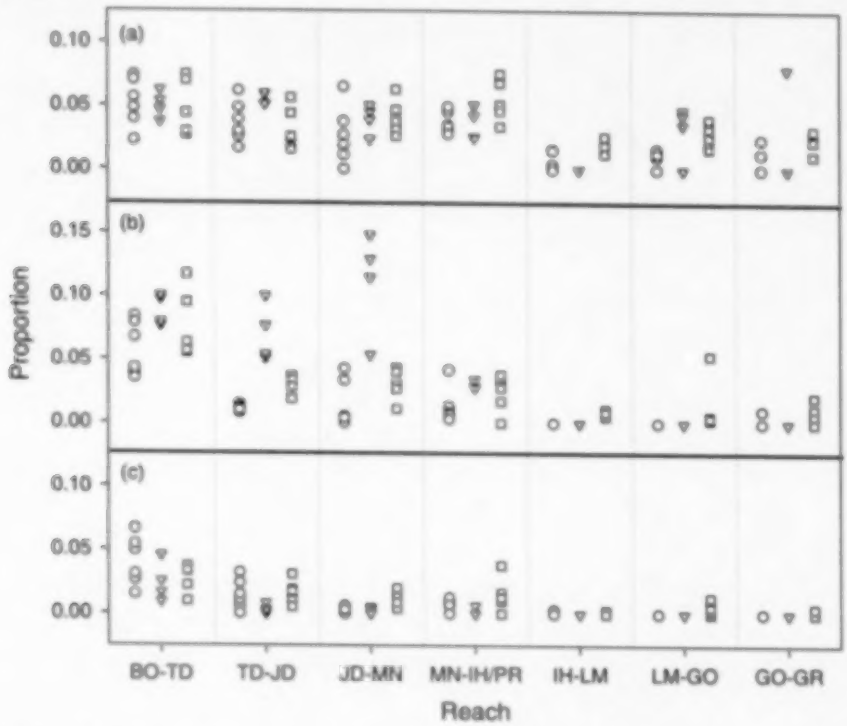
Fig. 6. Annual (1996–2002) estimates of proportions of radio-tagged chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) released downstream from Bonneville Dam that entered hydrosystem reaches and subsequently (*a*) had unknown fate (last recorded at a dam or in a reservoir), (*b*) were harvested in mainstem fisheries, or (*c*) were harvested in tributary fisheries. Circles, spring–summer chinook; triangles, fall chinook; squares, steelhead. Abbreviations for dams are as follows: BO, Bonneville; TD, The Dalles; JD, John Day; MN, McNary; IH, Ice Harbor; PR, Priest Rapids; LM, Lower Monumental; GO, Little Goose; GR, Lower Granite.



8.8%) and The Dalles – John Day (7.0%) reaches. Almost no chinook salmon and relatively few steelhead were harvested in the lower Snake River, but some fish from both species passed one or more Snake River dams and then migrated downstream and were harvested.

On average, 3%–5% of downstream-released fish from each run had unknown fates ($((U_i + U_d)(E_i)^{-1})$ after entering each lower Columbia River reach and <1%–3% had unknown fates after entering Snake River reaches. Resulting Esc_1 estimates for all runs were mostly between 0.930 and 0.980 for lower Columbia River reaches and were >0.950 for Snake River reaches (Fig. 5).

Known-source fish

Mean reach escapements for downstream-released known-source stocks from upper portions of the basin (Snake, Yakima, and upper Columbia) were typically higher than for the unknown-source mixed-stock samples, but patterns of escapement were similar (Fig. 7). Escapements for known-source upriver stocks from all runs were lowest through the Bonneville – The Dalles reach, were generally >0.900 through the other three Columbia River reaches, and were >0.970 through Snake River reaches for all groups except fall chinook salmon in 2001 (0.933, $n = 15$). Reach-specific estimates were not calculated for known-source chinook salmon from the John Day River ($n = 12$) or Wind River (stock did not fully pass any reach).

As with unknown-source groups, harvest of known-source fish was concentrated in lower Columbia River reaches. The highest single-reach harvest proportions for spring–summer chinook salmon were in the Bonneville – The Dalles reach (2002, Snake River = 7.3%; 2001, Yakima = 5.4%; 2002, upper Columbia = 4.1%). The highest proportions for steelhead were in the Bonneville – The Dalles reach (2001, Snake River = 5.6%) or The Dalles – John Day reach (2002, upper Columbia = 5.6%). The highest harvest rates for Snake River fall chinook salmon were in the John Day – McNary reach (15.4% in 2002) and Bonneville – The Dalles reach (7.7% in 2001). Snake River stocks of spring–summer chinook salmon tended to have lower escapements than upper Columbia River stocks through lower river reaches, reflecting greater harvest effort during the spring run when more Snake River fish are migrating. Few differences were seen between steelhead stocks, except Snake River fish were harvested in the Bonneville – The Dalles reach at higher rates than upper Columbia River fish (Fig. 7). As with hydrosystem escapement estimates, lower Columbia River reach estimates for known-source groups would be slightly lower if strays were treated as unsuccessful. Reach escapement estimates for forebay-released groups were generally

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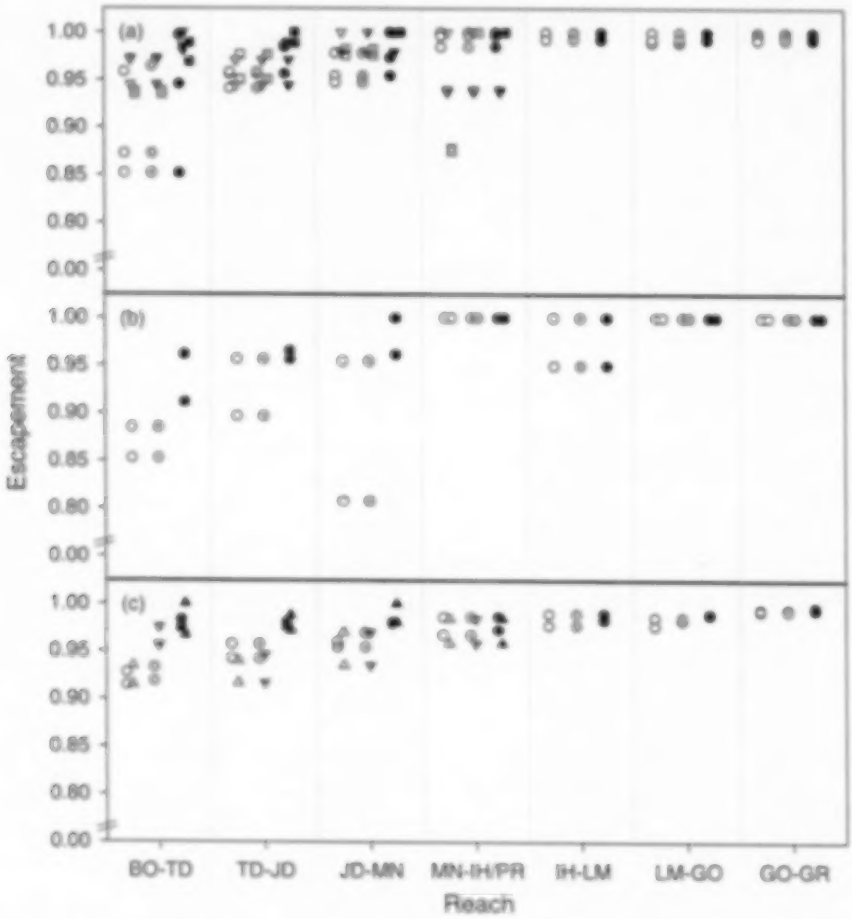
Fig. 7. Annual (2000–2002) reach-specific escapement estimates for known-source radio-tagged (*a*) spring–summer chinook salmon (*Oncorhynchus tshawytscha*), (*b*) fall chinook salmon, and (*c*) steelhead (*Oncorhynchus mykiss*) released downstream from Bonneville Dam. Circles, Snake River stocks; triangles, upper Columbia River stocks; squares, Yakima River stocks. Abbreviations for dams are as follows: BO, Bonneville; TD, The Dalles; JD, John Day; MN, McNary; IH, Ice Harbor; PR, Priest Rapids; LM, Lower Monumental; GO, Little Goose; GR, Lower Granite. Open symbols, Escapement 1 (Esc_1); dotted symbols, Escapement 2 (Esc_2); solid symbols, Escapement 3 (Esc_3).



similar to those for fish released downstream from Bonneville Dam. The exception was in the Bonneville – The Dalles reach, where escapement estimates tended to be lower for forebay-released fish.

Effects of fallback at dams

Unknown-source fish

Fallback at monitored hydrosystem dams had a consistent negative effect on fish escapement for fish from all runs and years (Table 5). On average, Esc_3 estimates were lower for fallback fish by 0.065 for spring–summer chinook salmon, 0.195 for fall chinook salmon, and 0.133 for steelhead. Differences were highly significant (χ^2 tests, $P < 0.005$) in all four fall chinook salmon runs, four of five steelhead runs, and the 1998 spring–summer chinook salmon run. Differences were significant at $P < 0.05$ for spring–summer chinook salmon in 1997 and 2000. Multiplication of the difference in Esc_3 estimates by system-wide fallback proportions indicated overall run escapement reductions ranging from 0.46% to 2.27% (mean = 1.30%) for spring–summer chinook salmon, from 1.32% to 2.91% (mean = 2.26%) for fall chinook salmon, and from 1.34% to 4.02% (mean = 2.84%) for steelhead (Table 5).

Known-source fish

Fallback effects for known-source stocks were similar to those for unknown-source samples (Table 5). Only six known-source groups had at least 10 fish that fell back during migration: Snake River spring–summer chinook salmon in all three years, Snake River steelhead in 2001 and 2002, and upper Columbia River steelhead in 2001. In all cases except 2001 upper Columbia River steelhead, non-fallback fish escaped at higher rates than fallback fish. Esc_3 differences (0.134–0.215) were significant ($P < 0.005$) for Snake River

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Table 5. Escapement 3 (Esc_3) estimates (n in parentheses) for downstream-released unknown-source and known-source fish that either were or were not recorded falling back (FB) over a monitored hydrosystem dam.

		Esc_3 estimate (n)				
Year	Stock	No fallback	Fallback	Esc_3 D^a	System FB (%)[b]	Esc_3 reduction ($D \times$ FB%)[c]
Spring–summer chinook salmon (*Oncorhynchus tshawytscha*)						
1996	Unknown	0.847 (632)	0.798 (178)	0.049	22.0	1.08
1997	Unknown	0.858 (683)	0.792 (269)	0.066**	28.3	1.86
1998	Unknown	0.881 (714)	0.784 (218)	0.097***	23.4	2.27
2000	Unknown	0.905 (702)	0.849 (186)	0.055**	20.9	1.15
2001	Unknown	0.931 (202)	0.840 (25)	0.091	11.0	1.00
2002	Unknown	0.931 (452)	0.901 (81)	0.030	15.2	0.46
2000	Snake River	0.824 (17)	0.700 (10)	0.124	37.0	4.58
2001	Snake River	0.967 (302)	0.833 (36)	0.134***	10.7	1.42
2002	Snake River	0.935 (138)	0.720 (25)	0.215***	15.3	3.29
Fall chinook salmon						
1998	Unknown	0.881 (805)	0.769 (108)	0.112***	11.8	1.32
2000	Unknown	0.894 (585)	0.635 (74)	0.259***	11.2	2.91
2001	Unknown	0.868 (438)	0.684 (57)	0.183***	11.5	2.11
2002	Unknown	0.914 (567)	0.688 (77)	0.225***	12.0	2.69
Steelhead (*Oncorhynchus mykiss*)						
1996	Unknown	0.780 (600)	0.702 (124)	0.078*	17.1	1.34
1997	Unknown	0.866 (700)	0.755 (216)	0.111***	23.6	2.62
2000	Unknown	0.882 (646)	0.774 (168)	0.108***	20.6	2.23
2001	Unknown	0.880 (276)	0.713 (87)	0.168***	24.0	4.02
2002	Unknown	0.872 (382)	0.670 (94)	0.202***	19.7	3.98
2001	Upper Columbia River	0.906 (170)	0.923 (13)	-0.017	7.1	-0.12
2001	Snake River	0.909 (186)	0.733 (45)	0.175***	19.5	3.41
2002	Snake River	0.897 (311)	0.809 (47)	0.089*	13.1	1.16

Note: Fallback after hydrosystem passage (top of Lower Granite or Priest Rapids dams) and known-source groups with fewer than 10 fallback fish excluded. The hydrosystem includes Bonneville, The Dalles, John Day, McNary, Ice Harbor, Lower Monumental, and Little Goose. *, $P < 0.10$; **, $P < 0.05$; ***, $P < 0.005$ (Pearson's χ^2 tests).

[a]Differences in Esc_3 estimates for fallback and nonfallback fish.

[b]Proportions recorded falling back at one or more dams.

[c]Overall Esc_3 reduction associated with fallback.

spring–summer chinook salmon in 2001 and 2002 and Snake River steelhead in 2001 (Table 5).

Effects of river environment

Unknown-source fish

Annual hydrosystem Esc_3 estimates for spring–summer chinook salmon were significantly and negatively correlated ($r^2 > 0.70$, $P < 0.04$) with mean and maximum Columbia River discharge during April–July (Table 6). Maximum discharge was also negatively correlated with mainstem harvest rates of spring–summer chinook salmon ($r^2 = 0.66$, $P = 0.050$), suggesting that escapement differences were not due to harvest effects. In contrast, discharge metrics were not correlated with annual hydrosystem Esc_3 estimates or mainstem harvest rates for either fall chinook salmon or steelhead during their migrations.

Water temperature means and maxima were not correlated with annual Esc_3 estimates for any of the three runs or with mainstem harvest rates for spring–summer chinook salmon or steelhead (Table 6). Harvest rates of fall chinook salmon were significantly higher in cooler years ($r^2 > 0.90$, $P < 0.05$) (Table 6), but the regression model was strongly influenced by the low harvest rate in 1998, when no fish were radio-tagged in August.

Discussion

This study used thousands of individual adult chinook salmon and steelhead migration histories to estimate escapement, distribution, harvest, and unaccounted for loss during spawning migrations through the Columbia River hydrosystem. The data provide quantitative insight into the biocomplexity that frames management of multispecies, multistock river systems. From the results, we believe that five important conclusions can be drawn. (*i*) Escapement indices for Columbia basin spring–summer and fall chinook salmon and steelhead varied significantly between species, between and within annual runs, and between some subbasin populations, (*ii*) high-discharge years corresponded to low spring–summer chinook salmon escapement, but neither discharge nor water temperature was consistently correlated with annual fall chinook salmon or steelhead escapement, (*iii*) mainstem harvest rates, especially in lower Columbia River reservoirs, differed between runs and may indicate un-

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Table 6. Linear regression results for models of seasonal mean (AVG) and maximum (MAX) river discharge and temperature and hydrosystem Escapement 3 (Esc_3) and mainstem harvest (MF) estimates for unknown-source radio-tagged fish.

	Years	r^2	P	β
Spring–summer chinook salmon (*Oncorhynchus tshawytscha*)				
Esc_3 vs.				
$Discharge_{AVG}$	6	0.73	0.030	–0.100
$Discharge_{MAX}$	6	0.71	0.035	–0.102
$Temperature_{AVG}$	6	0.06	0.631	0.024
$Temperature_{MAX}$	6	0.11	0.517	–0.017
MF vs.				
$Discharge_{AVG}$	6	0.57	0.085	–0.075
$Discharge_{MAX}$	6	0.66	0.050	–0.083
$Temperature_{AVG}$	6	0.01	0.836	0.009
$Temperature_{MAX}$	6	0.19	0.385	–0.019
Fall chinook salmon				
Esc_3 vs.				
$Discharge_{AVG}$	4	0.57	0.247	0.089
$Discharge_{MAX}$	4	0.53	0.275	0.061
$Temperature_{AVG}$	4	0.02	0.869	–0.003
$Temperature_{MAX}$	4	0.12	0.652	–0.007
MF vs.				
$Discharge_{AVG}$	4	0.01	0.925	–0.016
$Discharge_{MAX}$	4	0.04	0.801	–0.029
$Temperature_{AVG}$	4	0.91	0.046	–0.041
$Temperature_{MAX}$	4	0.92	0.042	–0.034
Steelhead (*Oncorhynchus mykiss*)				
Esc_3 vs.				
$Discharge_{AVG}$	5	0.31	0.327	–0.101
$Discharge_{MAX}$	5	0.34	0.303	–0.054
$Temperature_{AVG}$	5	0.12	0.562	0.048
$Temperature_{MAX}$	5	0.03	0.798	0.009
MF vs.				
$Discharge_{AVG}$	5	0.03	0.791	0.030
$Discharge_{MAX}$	5	0.00	0.970	0.002
$Temperature_{AVG}$	5	0.38	0.269	0.085
$Temperature_{MAX}$	5	0.60	0.127	0.045

Note: Environmental variables were for data at Bonneville Dam during the time that radio-tagged spring–summer chinook salmon (April–July), fall chinook salmon (August–October), and steelhead (June–October) were migrating. Discharge values were log-transformed.

acceptably high take of some US Endangered Species Act listed populations (e.g., upper Columbia River steelhead and Snake River fall chinook salmon), (*iv*) adult chinook salmon and steelhead that fell back over dams were significantly more likely to have unknown fates (presumed mortality) and lower hydrosystem escapement, and (*v*) reach (dam-to-dam) escapement estimates were lowest in the lower Columbia River and were highest in the lower Snake River. These findings help clarify patterns of adult fate during return migration, specifically for Columbia River chinook salmon and steelhead and more generally for anadromous salmonids.

Interpretation of such telemetry data is based on assumptions that tagged fish represent sampled populations and that tagged fish behave similarly to untagged fish. We made a concerted effort to proportionately and unselectively tag unknown-source fish from throughout each run. However, operational constraints and conflicting research priorities made strictly representative tagging impossible. Run size and timing, the location of the trapping facility (north shore only), and tagging stoppages (no summer chinook in July 1996 or fall chinook in August 1998) resulted in departures from representative sampling. We also sampled proportionately more late-migrating steelhead to have adequate samples of Snake River fish to address separate research objectives at Snake River dams. Collection of known-source groups was opportunistic and random and may also have been slightly biased because available fish likely did not fully capture stock diversity from basins they represented.

Despite these constraints, we believe that radio-tagged samples were good surrogates for the overall runs and that tagged fish behaved similarly to untagged fish. Radio-tagged chinook salmon had passage times through the hydrosystem (Bonneville Dam to Lower Granite Dam) similar to those of PIT-tagged salmon without radio tags (Matter and Sandford 2003), suggesting that tagging did not significantly affect migration behavior over long distances (~460 km). Run timing distributions of radio-tagged fish were also similar to those for all fish counted at dams, both at Bonneville Dam (Keefer et al. 2004*b*) and at upstream sites. In addition, the vast majority of radio-tagged fish in this study completed migration (Keefer et al. 2004*b*, 2004*c*) or could be accounted for in fisheries. This evidence of limited tagging effects was consistent with other adult salmonid telemetry research (Burger et al. 1985; Thorstad et al. 2000; Jokikokko 2002). A final concern in adult anadromous fish research, downstream movement following tagging (Bernard et al. 1999; Mäkinen et al. 2000), should not have substantively affected study results. Our focus on downstream-released fish should have ameliorated effects of retrograde movement, as escapement, harvest, and fate estimates were calculated only after fish volitionally resumed upstream migration and passed Bonneville Dam. Lower escapement by forebay-released fish (mean = 3.8% lower than for downstream releases, n = 27 pairs) may have represented initial transmitter loss, mortality following tagging, or fish destined for unmonitored sites downstream from Bonneville Dam.

The finding of significant escapement variation between species, years, seasons, and stocks was not unexpected. Survival during egg–fry, freshwater rearing, and marine life history stages varies widely among Pacific salmonids (Groot and Margolis 1991; Bradford 1995) as a result of environmental conditions like temperature and discharge, habitat quality, and both density-dependent and density-independent factors. Similar survival variance was also expected to occur for returning adults given the wide range of seasonal and annual river environments, run size, harvest schemata, and hydrosystem operations encountered during upstream migration. Large annual differences in within-run stock composition and timing (e.g., Keefer et al. 2004*b*) and overall Columbia basin stock diversity (Nehlsen et al. 1991; Waples et al. 2004) also support a predisposition to variable return migration success. The inter- and intra-annual escapement variability that we observed may have been related to intrin-

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sic stock-specific differences such as vulnerability to fisheries, susceptibility to adverse water temperatures (McCullough et al. 2001; Cooke et al. 2004), or underlying genetic characteristics (e.g., Unwin et al. 2003). Initial fish condition upon entering the hydrosystem, including fungal, disease, or parasite loads, frequency and severity of pinniped injuries (Harmon et al. 1994; Fryer 1998), and energetic reserves (Rand and Hinch 1998), may also have influenced observed escapement patterns.

The only strong escapement effect that we identified related to river environment was that spring–summer chinook salmon escaped at lower rates in high-discharge years. This may reflect general passage difficulty, increased fallback, delay, or orientation problems when flows are high or, more directly, bioenergetic exhaustion (Dodson 1997). Slowed and (or) failed migration due to depletion of energy reserves or difficult migration environments has been reported for sockeye (*Oncorhynchus nerka*) and pink salmon (*Oncorhynchus gorbuscha*) (Gilhousen 1990; Standen et al. 2002; Crossin et al. 2003), Atlantic salmon (*Salmo salar*) (Gerlier and Roche 1998; Gowans et al. 1999), and chinook salmon (Schreck et al. 1994; Geist et al. 2000). In contrast with spring–summer chinook salmon, annual escapement responses to measured environmental variables were not significant for fall chinook salmon or steelhead. We suspect, however, that more definitive patterns would emerge with longer data series (steelhead were studied for five years and fall chinook for four years). Water temperatures in the Columbia hydrosystem routinely reach levels that can reduce adult survival (McCullough 1999; McCullough et al. 2001), and compromised migrations might be expected given evidence from other studies (Major and Mighell 1967; Baigun et al. 2000; Cooke et al. 2004). Steelhead and fall chinook salmon, which migrate during peak temperatures in August and September, are the stocks most likely to have negative temperature-related impacts. Preliminary analyses using individual fish exposure histories and fates (as opposed to annual escapement estimates) suggest that more significant survival effects related to river environment can be detected with the telemetry database. Research at this individual-fish scale is in progress.

Although 12 Columbia basin salmon and steelhead stocks are listed as threatened or endangered (National Marine Fisheries Service 2000), mainstem mixed-stock fisheries continue in the Columbia and Snake rivers. Fisheries have been strictly managed in an effort to protect listed populations and reverse continued declines of native runs, with quotas set using predicted run size and run composition criteria and adjusted within seasons (Lestelle and Gilbertson 1993; Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 2000). Assessments of impacts on specific stocks, however, remain imprecise. Use of known-source fish in this study provided relatively specific information on the magnitude and distribution of stock-specific harvest upstream from Bonneville Dam. Data from the transmitter reward program suggest harvest rates of 9%–20% for endangered upper Columbia River steelhead, as high as 17% for threatened Snake River spring–summer chinook salmon, and as high as 25% for threatened Snake River fall chinook salmon. Actual harvest of these stocks was likely higher than indicated because we could only account for voluntarily reported harvest. Illegal and (or) unreported harvest did occur but was difficult to quantify with the telemetry data. The majority of radio-tagged known-source fish were hatchery derived but should have been good surrogates for comigrating wild evolutionarily significant unit populations because most harvest of these groups was in the lower hydrosystem in unselective, mixed-stock tribal fisheries. Further restrictions on the timing (e.g., Merritt and Roberson 1986; Hendry et al. 2002), distribution (McPherson et al. 2003), or selectivity of mainstem fisheries may be needed to enhance escapement, productivity, and recovery of the listed populations (Potter et al. 2003).

Following harvest, the greatest attributable loss of adult migrants was tied to fallback over dams. Adult fallback can result in longer hydrosystem passage times (Keefer et al. 2004*a*), greater energetic expenditures for reascending fish, possible impaired homing, and potential injury or mortality (Dauble and Mueller 1993, 2000). One or a combination of these factors may explain the significantly reduced escapement observed for unknown-source fallback fish (reductions of 3%–10% for spring–summer chinook salmon, 11%–26% for fall chinook salmon, and 8%–20% for steelhead). Escapement reductions for Snake River spring–summer chinook salmon and steelhead were even higher than for unknown-source groups, perhaps because these stocks must pass more dams than downstream stocks or because some (e.g., Snake River spring chinook salmon) migrated through the system when discharge was highest. The larger negative consequences for fall chinook salmon and steelhead, compared with spring–summer chinook salmon, may also have been a function of run timing. These migrations coincided with periods of reduced or zero spill at dams in fall when available fallback routes (through generating turbines or juvenile bypass systems) may be less benign than via spillways, the most-used route when spill occurs (Wagner and Hilsen 1992; Boggs et al. 2004).

The tendency for fallback to increase with discharge of the Columbia and Snake rivers (reviewed in Bjornn and Peery 1992) may partially explain the negative discharge–escapement relationship that we observed for spring–summer chinook salmon. Hydrosystem and dam-specific fallback rates were highest in high-discharge years (Boggs et al. 2004), coincident with the lowest spring–summer chinook escapement values. Parsing out what portion of the observed lowered escapement was directly due to discharge or indirectly to route searching or overshoot of natal tributaries was beyond the scope of this paper. We examined only hydrosystem-wide effects of fallback; dam-specific resolution of escapement impacts may yield more actionable results. Further research will be necessary to identify if fallback-related loss can be mediated through structural or operational hydrosystem modifications (e.g., Reischel and Bjornn 2003) and to describe what proportion of the loss can be attributed to initial fish condition, fish origin, juvenile rearing or transportation history, or other factors.

Partitioning fish fates for individual hydrosystem reaches indicated that greater attrition occurred for both species and all runs in lower portions of the hydrosystem. Dauble and Mueller (2000) also found reduced survival in lower Columbia River reaches relative to lower Snake River reaches.

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Using estimates of dam passage, harvest, hatchery return, and tributary turnoff, Dauble and Mueller (2000) calculated mean interdam conversions (1979–1998) for spring chinook salmon of 0.885 through lower Columbia River and 0.939 through lower Snake River reaches; means were 0.913 and 0.995, respectively, for summer chinook salmon. The current radiotelemetry results are likely more accurate, particularly in quantifying tributary turnoff and correctly accounting for multiple dam passage events and concomitant count inflation following fallback. Although methodologies differed, results were qualitatively similar and clearly indicated greater adult loss in the lower river. This pattern may reflect loss associated with unreported harvest, direct or delayed mortality following contact with fisheries, or more difficult passage environments at lower Columbia River dams or reservoirs. Among passage concerns, high fallback rates at Bonneville and The Dalles dams (Boggs et al. 2004), long passage times for all runs at John Day Dam (Keefer et al. 2004*a*), and slow passage and temporary straying by fall chinook salmon and steelhead (Gonica 2002; High 2002) may have direct escapement consequences.

Distinguishing between mortality and other fates is difficult for nonrecovered individuals in many survival studies for fish (e.g., Pahlke and Bernard 1996; Heupel and Simpfendorfer 2002) and other taxa (Francis and Saurola 2002; Bjorndal *et al.* 2003; Gardali et al. 2003). Animals not detected or recovered may have died, survived, emigrated to unsurveyed areas, been removed from the population through harvest, or survived yet been "unobservable" for biological or methodological reasons (Lebreton et al. 1992; Kendall and Nichols 2002). Additional possible false negatives for the radio-tagged adult salmonids in this study include undetected mainstem spawners and fish that lost transmitters. Hydrosystem escapement estimates here were principally derived from known survivors and known harvest within the monitored area. These estimates should therefore be accurate but may be considered minimums given uncertainty regarding the 12%–17% of each run with unknown fate. Some unknown-fate fish were likely harvested but not reported: had this harvest been identified, Esc_1 and Esc_2 estimates would have been unchanged, while Esc_3 estimates would have been higher. Other fish may have spawned at mainstem sites, although only very small aggregations of adults (mostly fall chinook salmon) spawn in hydrosystem reservoirs and dam tailraces (Dauble et al. 1999; Groves and Chandler 1999). Proportions of fish with unknown fates as a result of tag loss should also have been small. Mean transmitter regurgitation rates of 2%–4% were recorded for Snake River fish (Keefer et al. 2004*c*), but these fish were identified as successful in the escapement estimates, as were fish without radiotags that were collected at hatcheries or detected by PIT tag readers at upper Columbia River dams. A final component, undetected tributary entry or hydrosystem exit, should have been minimal given exceptional telemetry coverage at dams, in reservoirs, in hydrosystem tributaries, and upstream from the bounded study area. Detection efficiencies suggest that bias due to fate misclassification should have been minimal (Naughton et al. 2005).

Finally, we emphasize that hydrosystem escapement estimates do not directly translate to spawning escapements. Our treatment of the telemetry data did not address indirect or delayed effects of migration through the hydrosystem on spawning success. Many fish last detected in hydrosystem tributaries may not have successfully reached spawning sites, and some that reached spawning grounds may have died prior to spawning. Fish recorded passing the upper monitored boundaries of the monitored hydrosystem (Priest Rapids and Lower Granite dams) were considered successful migrants for this study, but distances from those dams to spawning sites can be considerable (e.g., more than 500 km for some Snake River stocks). Harvest, migration mortality, and prespawn mortality continue upstream from the bounds of this study and need to be factored into any spawning escapement estimates.

These results represent some of the most comprehensive fate, upstream passage, and escapement data ever collected for adult chinook salmon and steelhead. From the combined telemetry, fishery reward, and PIT tag databases, it was possible to quantify adult escapement variability, geographically and temporally partition harvest and loss, and contrast escapement patterns between species, runs, and specific stocks. Such summaries should aid managers working to fill gaps in understanding the adult ecology of upstream-migrating salmonids (Dauble and Mueller 1993, 2000; National Marine Fisheries Service 2000). Given the dramatic and continuing declines in wild Columbia basin salmon and steelhead (Kareiva et al. 2000; McClure et al. 2003), we believe that additional attention should be afforded returning adults. Small increases in adult escapement can directly increase productivity of wild and listed stocks, particularly given the large tracts of underused spawning and rearing habitat within the Columbia basin.

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Are characteristics of introduced salmonid fishes biased by propagule pressure?

Robert I. Colautti

Abstract: Many recent studies of nonindigenous species (NIS) have used life history and morphological characteristics of invaders to either (*i*) build statistical models that predict new invaders or (*ii*) test ecological and evolutionary hypotheses. However, species characteristics may be confounded if NIS are transported or introduced nonrandomly with respect to the chosen contrast group, which typically consists of native or globally available species. For example, deliberately introduced NIS are often chosen according to economic rather than ecological factors. Here, I use stocking records of salmonid species introduced into Nevada, USA, to test for propagule biases within this system. I find that established salmonids are introduced significantly more times, and in greater numbers, than are those that fail and that species chosen for introduction are a nonrandom sample of the global salmonid species pool. Statistical differences among characteristics of salmonid species that established, those that were introduced, and those from the global source pool suggest that maximum reported size and weight as well as latitudinal range and midlatitude all represent propagule-biased characteristics of salmonids introduced into Nevada. These results highlight the need for caution when using characteristics of invaders to develop statistical models or to test hypotheses relevant to ecology and evolution.

Résumé : Plusieurs études récentes sur les espèces non indigènes (NIS) utilisent le cycle biologique ou les caractéristiques morphologiques des envahisseurs ou bien (*i*) pour élaborer des modèles statistiques de prédiction de nouvelles invasions, ou alors (*ii*) pour éprouver des hypothèses écologiques ou évolutives. Cependant, les caractéristiques spécifiques des NIS peuvent être obscurcies par rapport à leur groupe de comparaison, qui consiste ordinairement d'espèces indigènes ou d'espèces cosmopolites, lorsque les NIS sont déplacées ou introduites de façon non aléatoire. Par exemple, les NIS introduites délibérément sont souvent choisies pour des motifs économiques plutôt qu'écologiques. Les données d'empoissonnement de salmonidés au Nevada, É.-U., servent ici à évaluer les distorsions reliées aux propagules dans ce système. Les salmonidés qui se sont établis ont été introduits à plus de reprises et en plus grands nombres que les espèces qui ne se sont pas établies; de plus, les espèces choisies pour l'empoissonnement ne forment pas un échantillon aléatoire de l'ensemble global des espèces de salmonidés. Les différences statistiques entre les caractéristiques des espèces établies, celles des espèces introduites et celles de l'ensemble global laissent croire que la taille et la masse maximales signalées, ainsi que l'étendue et le point central de la répartition géographique, représentent tous des distorsions liées aux propagules dans les caractéristiques des salmonidés introduits au Nevada. Ces résultats montrent qu'il faut faire preuve de prudence quand on utilise les caractéristiques des envahisseurs pour élaborer des modèles statistiques ou tester des hypothèses d'intérêt écologique ou évolutif.

[Traduit par la Rédaction]

Introduction

Nonindigenous species (NIS) can effect profound changes to natural and agricultural ecosystems and are therefore of particular interest to conservationists and environmental economists (Mack et al. 2000; Pimentel et al. 2002; Rahel 2002). In addition, biological invasions are natural experiments with results relevant to both ecology and evolution (Richardson 1998; Evans et al. 2001). The process by which species invade can be conceptualized as a series of stages, beginning with a potential pool of invaders. From this source pool, only a subset of species will be transported to new areas, where some may be released, and of those, a few may establish viable populations; after establishment, some species may spread or increase in abundance within their new range (Williamson 1996; Richardson et al. 2000; Kolar and Lodge 2001). Here, I am concerned with the early stages of invasion: transport from a source region, introduction into a novel area, and establishment of a viable population (stages 0–III sensu Colautti and MacIsaac 2004).

To aid prediction and control of biological invasions, ecologists have sought generalities among patterns of NIS establishment, spread, and impact. In particular, much research has focused on identifying the characteristics associated with NIS that successfully establish in novel habitats or those that threaten natural ecosystems, often in the form of statistical models that are intended to predict future invaders (e.g., Williamson and Fitter 1996; Goodwin et al. 1999; Kolar and Lodge 2002). Despite the large number of studies that have identified characteristics of particular taxa in particular regions, broader generalizations are conspicuously rare (Williamson 1996; Kolar and Lodge 2001; Daehler 2003).

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R.I. Colautti. Botany Department, University of Toronto, 25 Willcocks Street, Toronto, ON M5S 3B2, Canada (e-mail: colautti@botany.utoronto.ca).

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Nevertheless, an understanding of the factors that determine which species will invade is of great importance to the development of ecological theory and to the success of management strategies.

Also important, but often overlooked, is the role of transport vectors and pathways in determining patterns of NIS establishment (Kolar and Lodge 2001; Duncan et al. 2003; Ruiz and Carlton 2003). This line of reasoning is based on the "propagule pressure" concept, which relates the establishment success of NIS to the density of individuals introduced, the number of introduction events, and the frequency of introductions (Williamson 1996; Lonsdale 1999; Kolar and Lodge 2001). Propagule pressure remains largely overlooked among recent invasion studies but holds potential for predicting and preventing future invasions. More importantly, nonrandom variation in propagule pressure may confound patterns of NIS establishment in general and characteristics of NIS in particular (Duncan et al. 2003; Cassey et al. 2004; Colautti and MacIsaac 2004). I use the term propagule bias to describe any pattern of invasion (e.g., the body size of invasive salmonids) that is confounded by nonrandom variation in propagule pressure (e.g., only big fish are introduced). In principle, patterns apparent at any stage of the invasion process can be confounded by propagule pressure at any preceding stage (Colautti and MacIsaac 2004). For example, Cassey et al. (2004) noted that the characteristics of established parrots (Psittaciformes) changed with the choice of contrast group because species chosen for transport and introduction were nonrandom selections of the source pool of potential invaders.

Identification of propagule biases can be challenging because accurate measurements of propagule pressure are usually not available. One exception is when deliberate introduction events are recorded by government agencies, acclimatization societies, and other organizations. Based on historical records of passerine bird and ungulate mammal introductions, several studies suggest that propagule pressure is an important determinant of invasion success (reviewed in Duncan et al. 2003; also see Forsyth and Duncan 2001; Cassey et al. 2004), likely confounding the ecological and evolutionary explanations used to describe invasion patterns (e.g., see Duncan 1997; Moulton et al. 2001; Duncan and Blackburn 2002). Moreover, measurements of propagule pressure, both the number of propagules introduced and the number of introduction events, proved to be the best predictors of establishment success in these studies. However, to the best of my knowledge, no such assessments have been done on aquatic systems.

Salmonid fishes have been widely introduced throughout North America and Europe, likely owing to their economic importance to both commercial and recreational fisheries (Crossman 1991; Holčík 1991). Several studies have identified characteristics of nonindigenous fishes, including salmonid species, but have not considered the potential for confounding effects of propagule biases (e.g., Marchetti and Moyle 2001; Kolar and Lodge 2002; Vila-Gispert and Moreno-Amich 2003). Here, I use records of salmonid introduction compiled by Miller and Alcorn (1946) for the state of Nevada, USA, and several traits obtained from FishBase (www.fishbase.org) to test the potential for propagule biases of introduced salmonids.

Methods

Propagule pressure

Miller and Alcorn (1946) reviewed government records on salmonid introductions for both successful and failed invasions in Nevada between 1873 and 1942. Data from this source include records on the number of propagules introduced as eggs, fingerlings, or unreported life stages. The authors also summarized the number of propagules "transported" into the state for purposes of introduction but often without confirmation of their ultimate fate. For measurements of propagule pressure, I included both the number of propagules recorded as introduced and the number of those transported for the purpose of introduction except in cases where shipped propagules arrived dead or severely harmed. I also tallied the number of discrete introduction events reported for each species. Thus, I examined two component measurements of propagule pressure: the number of individuals and the number of discrete introduction events.

In addition to salmonid species and subspecies, Miller and Alcorn (1946) reported data for species in other fish families. However, I constrained the analysis to salmonids for four main reasons: (*i*) examination of closely related taxa reduces (but does not eliminate) confounding effects of phylogenetically inherited traits among distinct lineages (see Felsenstein 1985; Miles and Dunham 1993), (*ii*) salmonids have historically been introduced primarily by government agencies or professional organizations, and introductions were therefore often well documented, (*iii*) salmonids generally require a higher degree of effort and expertise to rear for introduction, particularly given transportation technology before 1942. This reduces the possibility of private, unrecorded introductions relative to other species (e.g., centrarchids and cyprinids), and (*iv*) protocols for salmonid introductions have been fairly well developed; therefore, most propagules are likely to have been introduced only into appropriate habitats following similar protocols, thereby reducing confounding effects of environment.

For the purposes of this study, I characterized as nonindigenous all species that were deliberately moved beyond their native range. I therefore did not distinguish between species native to other continents, countries, American states, or other parts of Nevada. FishBase was used as the taxonomic authority except where Miller and Alcorn (1946) reported subspecies not recognized by FishBase. In these cases, I used the subspecies to test propagule pressure but not species-specific characteristics.

Species characteristics

I used data available from FishBase to compile a list of globally available salmonids not introduced into Nevada (161 species). For these species and those identified in Miller and Alcorn's (1946) study (16 subspecies representing 13 species), I compiled the maximum reported size (cm), weight (kg), and age (years) for each species as well as the temperature ranges (°C) and the ranges of latitude (°) at which each species occurred. Records were treated at the subspecies level unless data were only available at the level of species. One hybrid in the data set, *Oncorhynchus mykiss irideus* × *Oncorhynchus clarki henshawi*, was treated as *O. mykiss* for all analyses, primarily to reduce renduncy with

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Table 1. An R × C contingency analysis of taxonomic representation of introduced salmonid genera.

Genus	No. of species: Global pool	Introduced	Total	% introduced
Coregonus	61	1	62	1.61
Oncorhynchus	7	7	14	50.0
Salmo	25	2	27	7.41
Salvelinus	37	2	39	5.13
Thymallus	4	1	5	20.0

$G_{adj} = 9.97$, $\chi^2_{[0.05,4]} = 9.49$

O. clarki. I also recorded the average temperature at which each species occurred, except where an average was not given, in which case, I used the midpoint of the maximum and minimum recorded temperatures. Finally, I calculated the latitudinal midpoint for the geographical range of each species; therefore, average temperature and latitudinal midpoint may not be independent of temperature range and latitudinal range, respectively. Together, these data represent a number of characteristics for three groups of salmonids: those that were confirmed as established in Nevada, those that were introduced but not known to be established (hereafter referred to as failed invaders), and those comprising the global list of known salmonid species (the global source pool).

Status as established or failed reported in Miller and Alcorn (1946) was assumed to be accurate. It is possible that the status of some species may have changed since 1946, but an updated list would require an extensive review of introduction attempts after 1942. Moreover, technological improvements to transportation and increases in human density are likely to have increased the number of unreported introductions since then.

Statistical tests

I first tested whether introduced salmonid genera were taxonomically over- or under-represented. Taxonomic overrepresentation describes a genus that contains more species than would be expected from a random sample of the globally available species pool (see Lockwood 1999). A total of 16 subspecies representing 13 species were introduced, of which seven subspecies (from five species) established; this small sample size precluded a comparison of taxonomic representation between the established and failed groups of salmonids but allowed comparison between introduced species and those from the global pool. I then conducted separate Student's *t* tests on both the number of introduction events and the number of propagules per introduction for established and failed salmonids to test whether successful subspecies were introduced more times or in greater numbers than the failed group. The numbers of propagules introduced per attempt were log transformed to normalize the variance. Finally, I ran analysis of variance tests for each species characteristic examined among the three groups (established, failed, and global pool) with a Tukey post hoc test on significant results. Characteristics taken from FishBase were available only at the species level in many cases, such as *O. clarki* subspecies. Therefore, I excluded *O. clarki* subspecies (three established and one failed) from all analyses except for the propagule pressure comparisons. To test for taxonomic over- or under-representation, I conducted an R × C contingency table using a *G* test statistic and a Williams correction following Sokal and Rohlf (1995). All other statistical tests were run using the Systat 7.0.1 software package from SPSS Inc. (Chicago, Illinois).

Data from FishBase were not available for the temperature range of any of the established salmonids, and most species were missing one or more characteristics (Appendix A). This precluded multivariate analyses such as a generalized linear model or multivariate analysis of variance among traits (see Blackburn and Duncan 2001; Cassey et al. 2004).

Results and discussion

To test for propagule biases among characteristics of nonindigenous salmonids, I contrasted three groups: (*i*) salmonid fishes that were introduced and successfully established viable populations, (*ii*) salmonids that were introduced but failed to establish, and (*iii*) all other salmonid species listed on FishBase (the global pool). Comparisons between introduced salmonids (both established and failed species) and the global pool will identify propagule biases at the transport stage of the invasion process (i.e., stage I sensu Colautti and MacIsaac 2004). To identify propagule biases of introduction (stage II), I can draw comparisons between characteristics of introduced species that established and those introductions that failed, only if a significant difference in propagule pressure between the groups is found.

Contingency analysis of taxonomic representation by introduced salmonid genera revealed a statistically significant difference between species chosen for introduction and those available globally ($p < 0.05$, Table 1). For example, the single *Coregonus* species chosen for introduction represents only about 1.6% of all *Coregonus* species globally, while the six *Oncorhynchus* species represent 50% of the genus. Biases in species chosen for introduction should not be surprising, since the economically valuable trout, salmon, and char species belong primarily to the *Oncorhynchus*, *Salmo*, and *Salvelinus* genera. Conversely, the *Coregonus* genus represents many of the less economically important cisco and whitefish species. However, more cryptic biases are also possible. For example, species may be chosen from particular geographic areas or chosen according to habitat requirements, although data from FishBase are insufficient to test this.

Established subspecies were indeed introduced significantly more times ($p = 0.039$) and in greater numbers ($p = 0.011$) than were salmonid subspecies that failed to establish (Fig. 1). This separation is most easily visualized by the small degree of overlap between the two groups when plotted with discrete introduction events on the *x* axis and the log-transformed number of propagules introduced on the *y* axis (Fig. 2). This clear difference in propagule pressure between the established and failed groups suggests propagule-biased patterns of introduced species (stage II). Thus, two types of propagule biases exist in this study: one due to the nonrandom selection of salmonids from the global

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Fig. 1. Mean number of introduction events and log-transformed mean number of individuals introduced for established (solid bars) and failed (open bars) invaders. Both comparisons were statistically significant according to Student's t test ($p < 0.05$). Error bars represent +1 SE.

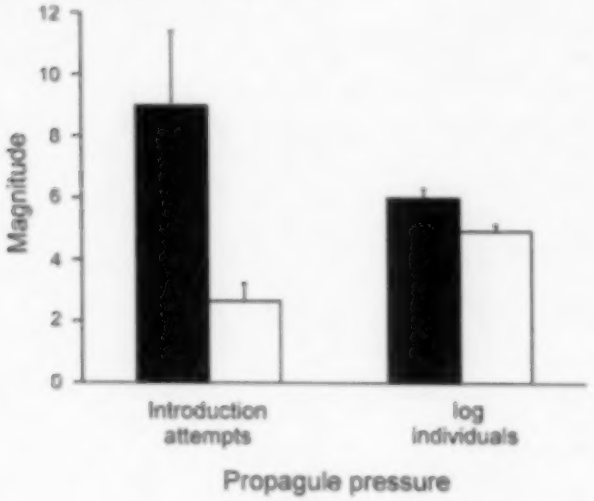
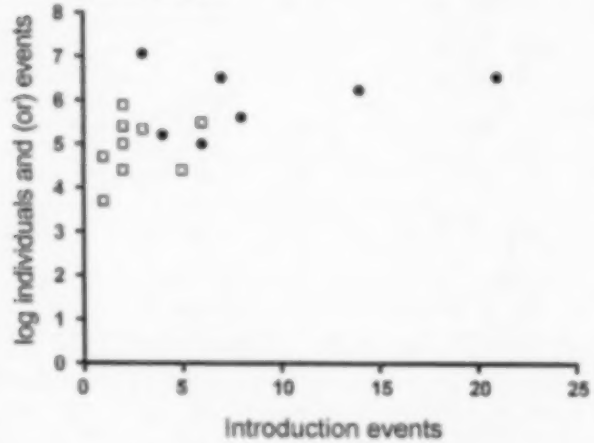


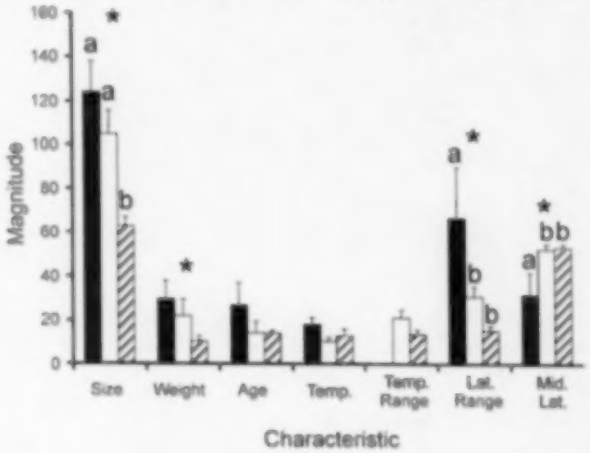
Fig. 2. Scatterplot of two components of propagule pressure showing strong separation between established (circles) and failed (squares) invaders.



pool for introduction (stage I) and one from a disproportionate introduction effort for successful invaders (stage II).

A number of characteristics were significantly different among the three groups; these represent potential propagule biases given the nonrandom selection of introduced species and the disproportionate introduction effort for established species (Fig. 3). Four characteristics, namely maximum reported size ($p < 0.001$) and weight ($p = 0.04$) as well as midlatitude ($p < 0.001$) and latitudinal range ($p = 0.002$), were significantly different. Additionally, the average temperature for each species was marginally significant ($p = 0.067$). After a Bonferroni correction, only weight became nonsignificant, but given the small sample size, I caution

Fig. 3. Means (+1 SE) of characteristics measured for established (solid bars) and failed (open boxes) invaders as well as those representing the global source pool (hatched bars). Maximum reported size, maximum weight, latitudinal range, and latitudinal midpoint all yielded significant differences based on separate analysis of variance tests ($p < 0.05$). Asterisks denote significant characteristics based on analysis of variance tests. Lowercase letters show the results of Tukey's post hoc test.



against a conclusive dismissal of propagule bias for marginally significant results. In other words, propagule pressure may bias characteristics of introduced salmonids, even though the number of species introduced is too small to detect this difference statistically.

Based on post hoc tests, maximum reported size is a candidate for propagule bias at transport and introduction stages (stages I and II) because species chosen for introduction (i.e., both the established and failed groups) were significantly bigger than those from the global species pool (Fig. 3). One explanation is that economically desirable species may be, on average, larger than less desirable species, resulting in a higher likelihood of human transport and higher overall propagule pressure. This may be explained by the economic importance of large salmonids to commercial and recreational fisheries, for example. Latitudinal range and midlatitude are also strong candidates for propagule biases. Although only of marginal significance, both maximum weight and temperature range may also be propagule biased, but not detectable given the small sample size. Similarly, trends (in Fig. 3) that were not significant according to post hoc testing may be attributable to propagule biases that are not detectable due to small sample size. For example, size showed a decreasing trend from established species to failed species to the global pool of salmonids, but only the latter was significantly different. Weight also showed a significant declining trend, but with no significant difference based on Tukey's post hoc pairwise comparisons (Fig. 3).

Most characteristics of nonindigenous salmonid species contrasted in this study were therefore correlated with propagule pressure among each contrast group (Fig. 3). Maximum reported size, weight, temperature range, latitudinal range, and midlatitude are potentially biased at the transport and introduction stage (stages I and II) because the

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Table 2. Mean morphological and habitat characteristics of established, failed, and other (global pool) salmonids.

	Size (cm)	Weight (kg)	Age (years)	Average temperature (°C)	Temperature range (°C)	Latitudinal range (°)	Midlatitude (°)
All species							
Established	124	29.37	27	18.0		67	31.4
Failed	105	21.85	14	10.6	21	31	52.3
Global pool	63	10.43	14	12.9	14	15	53.0
***Oncorhynchus* species only**							
Established	120	25.40	11	17.0		32	47.5
Failed	103	21.04	7	12.4	25	30	50.5
Global pool	57	4.14	3	21.0		12	42.6
***Oncorhynchus* species excluded**							
Established	125	30.70	32	18.6		78	26.0
Failed	109	23.21	27	3.5	7	32	55.3
Global pool	63	11.52	14	11.2	14	16	54.8

Note: Results were calculated for all species, for *Oncorhynchus* species only, and for all species not belonging to the *Oncorhynchus* genus. Characteristics are the same as in Fig. 3.

characteristics of species chosen for introduction, whether established or failed, appear to be nonrandom samples of the global species pool. Latitudinal range, midlatitude, and possibly size and weight are potentially biased at the stage of introduction (stage II) because characteristics associated with species that establish are also characteristic of those that are introduced more often and in greater numbers (Figs. 1–3).

It is possible that my results are biased by the nonindependence of characteristics among related species and subspecies. In particular, six of the nine failed introductions were species in the *Oncorhynchus* genus. Low sample size of introduced species and uncertain phylogenetic relationships for many species in the global pool make a comprehensive, phylogenetically controlled analysis difficult. However, characteristic means are qualitatively similar when *Oncorhynchus* species are excluded and for *Oncorhynchus* species only (Table 2), although sample size is too small to test this statistically. It is nonetheless conceivable that significant characteristics could vary among analysis techniques. However, my key finding is not dependent on the specific characteristics that differ between the established, failed, and global pool groups. Rather, it is the implication that characteristics of successfully established NIS are likely to be biased by nonrandom selection from a source pool and disproportionate variation in propagule pressure (Table 1; Figs. 1 and 2) that underlie deliberate introductions of salmonids in particular and NIS in general. Independent of the analysis techniques that could be used, the results presented suggest that the biological significance of characteristics of established salmonids (and perhaps deliberately introduced NIS in general) should be considered cautiously.

Given the number of differences in this rather small data set, propagule biases may be much more common than is generally acknowledged, particularly given that many NIS have been intentionally introduced according to human decision (Ruiz and Carlton 2003). Several studies have identified characteristics of introduced fishes (e.g., Moyle and Light 1996; Marchetti and Moyle 2001; Vila-Gispert and Moreno-Amich 2003) and other species (e.g., Goodwin et al. 1999; McGlynn 1999; McMahon 2002) but have not considered the potentially confounding effects of propagule pressure. The results presented here stress the importance of such a consideration for deliberately introduced species. However, an analogous propagule bias is expected for accidentally introduced species if introduction and transport vectors sample propagules nonrandomly. For example, a comparison of characteristics between native species and NIS introduced into the Laurentian Great Lakes in ballast effluent could be confounded by characteristics that promote a species uptake into, and survival in, ballast tanks (e.g., physiological tolerance, high fecundity, and pelagic life stage). Confounded characteristics may be more cryptic if, for example, other characteristics (e.g., body size and life span) are correlated with those promoting uptake and survival. Quantifying such biases could be very difficult where historical records are unavailable. However, a careful analysis of transport and introduction vectors might be used as a correlate of propagule pressure where accurate data are unavailable (e.g., Wonham et al. 2000; Grigorovich et al. 2003; Ruiz and Carlton 2003).

The data presented here are purely correlative, and it is therefore impossible to confirm propagule bias as the primary driver of salmonid characteristics. It is conversely possible that the characteristics of species chosen for introduction, and those of species that establish viable populations, are indicative of underlying ecological or evolutionary principles and that patterns of propagule pressure are spuriously correlated due to human activity. The alternative hypotheses can be more easily articulated as a question: do certain salmonid subspecies establish because they are introduced more times and in greater numbers or are they introduced more because they are better at establishing? Several lines of reasoning suggest that the evidence for propagule bias is real, or at least should be assumed so. First, I would argue that of the two explanations, propagule pressure is the more parsimonious and has the potential to confound any NIS characteristics that may be cited to support ecological or evolutionary hypotheses. Thus, it is more logical to test for propagule bias prior to those pertaining to physiological capability of species to establish (Rahel 2002; Duncan et al. 2003; Cassey et al. 2004). Second, several experimental

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studies have confirmed the importance of the number of propagules and the number of introduction events to establishment (Ebenhard 1989; Memmott et al. 1998; Grevstad 1999). Third, propagule biases have also been implicated for introduced ungulates and several bird species, although in all cases, species were deliberately introduced (Forsyth and Duncan 2001; Duncan et al. 2003; Cassey et al. 2004). Fourth, species are often chosen for introduction based on economic rather than ecological considerations per se. Finally, the alternative hypothesis can discount propagule biases at the establishment stage but poorly explains why even failed species appear to be nonrandom samples (Fig. 3). It is also worth noting, although anecdotal, that of the four *O. clarki* subspecies identified by Miller and Alcorn (1946) that were introduced, only one subspecies (*O. clarki stomias*) failed to establish. It was introduced only once, and the number of individuals introduced was almost 100-fold less than that of any of the three subspecies that established (Appendix A).

At the very least, the correlation between propagule pressure and characteristics of introduced and established salmonids should be a cause for concern when inferring ecological and evolutionary processes based on species characteristics or parameters correlated with them (e.g., population growth rate and competitive ability). Similarly, the predictive value of statistical models for future invaders should be interpreted with caution because temporal changes to propagule pressure may alter patterns of invasion, for example, if humans suddenly chose to introduce small salmonids instead of large species.

Perhaps a failure to identify propagule biases can help to explain the lack of generalizations on characteristics of "good" invaders or the phenomenon that closely related species often vary drastically in their "ability" to invade novel habitats (Williamson 1996). The importance of considering hypotheses based on the propagule pressure concept cannot be overstressed, as virtually any type of invasion analysis is potentially prone to propagule bias. Most importantly, an approach to invasion modelling that incorporates, at its core, variation in propagule pressure can only improve our ability to predict and prevent future invasions.

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Appendix A

Table A1. List of known salmonid species.

	A	B	C	D	E	F	G	H	I
Established									
Salmo trutta ***fario***	8	410 250	140	50.00	38	24.1		104	16.5
Oncorhynchus clarki ***henshawi***	14	1 737 190	99	18.60	10	23.2		22	50.5
Oncorhynchus clarki lewisi	7	3 256 480							
Oncorhynchus clarki ***utah***	3	11 386 614							
O. mykiss ***irideus*** × *O. clarki* ***henshawi***	4	159 785	120	25.40	11	17.0		32	47.5
Salvelinus fontinalis ***fontinalis***	21	3 474 345	86	9.39	7	13.0		22	50.5
Salvelinus namaycush ***namaycush***	6	100 245	150	52.70	50			109	11.0
Failed									
Thymallus arcticus ***tricolor***	1	50 130	76	3.83	18			31	59.0
Coregonus clupeaformis ***clupeaformis***	2	25 000	100	19.00	50			32	55.5
Salmo salar ***sebago***	5	25 000	150	46.80	13	3.5	7	34	51.5
Oncorhynchus clarki ***stomias***	1	4 925							
Oncorhynchus aguabonita	2	250 000	71	4.98	7			2	36.5
Oncorhynchus keta	3	213 000	100	15.90	6	12.0	24	40	52.5
Oncorhynchus tshawytscha	6	310 000	150	61.40	9	12.5	25	36	54.5
Oncorhynchus kisutch	2	100 000	108	15.20	5	12.5	25	36	54.5
Oncorhynchus nerka	2	765 000	84	7.71	7	12.5	25	36	54.5
Global pool									
Acantholingua ohridana				0.69	12				
Brachymystax lenok			70	8.00					
Brachymystax savinovi									
Coregonus albellus									
Coregonus albula			45	1.00	10			16	65.5
Coregonus alpinus									
Coregonus arenicolus									
Coregonus artedi			57	3.35	11	13.0	26	26	56.5
Coregonus atterensis			40						
Coregonus autumnalis autumnalis			64						67.5
Coregonus autumnalis migratorius			56			6.0	12		
Coregonus bavaricus									

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Table A1. (*continued*).

	A	B	C	D	E	F	G	H	I
Coregonus bezola									
Coregonus candidus									
Coregonus chadary			59						
Coregonus clupeoides									
Coregonus confusus									
Coregonus danneri									
Coregonus fatioi									
Coregonus fera									
Coregonus gutturosus									
Coregonus heglingus									
Coregonus hiemalis									
Coregonus hoferi									
Coregonus hoyi			37		10				
Coregonus huntsmani			40					2	43.5
Coregonus johannae									
Coregonus kiyi			35		10				
Coregonus laurettae			36					12	63.5
Coregonus lavaretus			70	10.00		6.0	12	34	56.5
Coregonus lavaretus baicalensis			60						
Coregonus lucidus									
Coregonus lucinensis									
Coregonus macrophthalmus									
Coregonus maraena			130	10.00					
Coregonus maxillaris									
Coregonus megalops									
Coregonus muksun			64	13.80	23			5	71.0
Coregonus nasus			71	16.00	15			15	66.0
Coregonus nelsoni			56					10	63.5
Coregonus nigripinnis			39		14				
Coregonus nilssoni									
Coregonus nobilis									
Coregonus oxyrinchus			50	2.00		8.0	16	7	54.0
Coregonus palaea									
Coregonus pallasii			46						
Coregonus peled			50	5.00					
Coregonus pennantii									
Coregonus pidschian			46		14			12	65.5
Coregonus pollan			35	0.45	10			4	53.5
Coregonus reighardi			36	0.54	8				
Coregonus renke									
Coregonus restrictus									
Coregonus sardinella			47	0.56	26			34	58.5
Coregonus stigmaticus									
Coregonus subautumnalis			37.5						
Coregonus suidteri									
Coregonus trybomi									
Coregonus tugun			20						
Coregonus tugun lenensis			15.9						
Coregonus ussuriensis			52						
Coregonus vandesius									
Coregonus wartmanni			50				11	2	47.5
Coregonus widegreni			50	2.00					
Coregonus zenithicus			40		11			21	52.0
Coregonus zuerichensis									
Coregonus zugensis									
Hucho bleekeri			64						
Hucho hucho			150	52.00	15		12	16	47.5

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Table A1. *(continued).*

	A	B	C	D	E	F	G	H	I
Hucho ishikawae			50						
Hucho perryi			200	5.75				9	46.0
Hucho taimen			160	70.00	16				
Oncorhynchus apache			58	2.36				2	33.5
Oncorhynchus chrysogaster									
Oncorhynchus gilae			32					3	34.0
Oncorhynchus gorbuscha			76	6.80	3	21.0		46	49.5
Oncorhynchus ishikawai								2	34.5
Oncorhynchus iwame									
Oncorhynchus masou formosanum									
Oncorhynchus masou macrostomus			50	1.54					
Oncorhynchus masou masou			71	10.00				8	61.5
Oncorhynchus masou rhodurus									
Prosopium abyssicola			28					2	41.5
Prosopium coulteri			28		9			13	53.0
Prosopium cylindraceum			59	2.70	16			29	57.0
Prosopium gemmifer			22		6			2	41.5
Prosopium spilonotus			56		8				
Prosopium williamsoni			70	2.92	14	23.2		30	53.5
Salmo aphelios									
Salmo balcanicus									
Salmo carpio									
Salmo cettii									
Salmo dentex									
Salmo ezenami									
Salmo fenox									
Salmo fibreni							1		
Salmo ischchan			104	17.00					
Salmo labrax			110						
Salmo letnica				0.01					
Salmo lumi									
Salmo macedonicus									
Salmo marmoratus							23		
Salmo nigripinnis									
Salmo pelagonicus									
Salmo penshinensis			96						
Salmo peristericus									
Salmo platycephalus									
Salmo rhodanensis									
Salmo schiefermuelleri									
Salmo stomachicus									
Salmo taleri									
Salmo visovacensis									
Salmo zrmanjaensis									
Salmothymus obtusirostris								4	41.5
Salvelinus agassizi									
Salvelinus albus									
Salvelinus alpinus			107	15.00	40		12	44	63.5
Salvelinus alpinus erythrinus			70						
Salvelinus anaktuvukensis			30		9				
Salvelinus andriashevi			29.9						
Salvelinus boganidae			46.5						
Salvelinus colii									
Salvelinus confluentus			103	14.50				23	50.0
Salvelinus czerskii									
Salvelinus drjagini			90	8.30					
Salvelinus elgyticus				0.11					

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Table A1. (*concluded*).

	A	B	C	D	E	F	G	H	I
Salvelinus fimbriatus									
Salvelinus gracillimus									
Salvelinus grayi									
Salvelinus inframundus									
Salvelinus jacuticus									
Salvelinus japonicus								3	34.0
Salvelinus killinensis									
Salvelinus leucomaenis imbrius									
Salvelinus leucomaenis leucomaenis			80	7.37				19	51.0
Salvelinus leucomaenis pluvius			83						
Salvelinus lonsdalii									
Salvelinus mallochi									
Salvelinus malma krascheninnikova			75						
Salvelinus malma malma			127	18.30			14	24	59.5
Salvelinus malma miyabei			70						
Salvelinus maxillaris									
Salvelinus murta									
Salvelinus neiva			55						
Salvelinus obtusus									
Salvelinus perisii									
Salvelinus profundus									
Salvelinus scharffi									
Salvelinus struanensis									
Salvelinus thingvallensis									
Salvelinus tolmachoffi			37						
Salvelinus trevelyani									
Salvelinus umbla									
Salvelinus willoughbii									
Salvelinus youngeri									
Salvethymus svetovidovi									
Stenodus leucichthys			150	40.00	22			16	65.5
Thymallus brevirostris			39						
Thymallus nigrescens			30.6						
Thymallus thymallus			60	6.70	14		12	25	54.0
Thymallus yaluensis			20						

Note: The number of (A) introduction events and (B) individual propagules introduced are listed for introduced salmonid subspecies that established in Nevada and those that failed to establish viable populations according to Miller and Alcorn (1946). Also listed are characteristics reported from FishBase (www.fishbase.org): (C) maximum reported length (cm), (D) maximum reported weight (kg), (E) maximum reported age (years), (F) mid- or mean temperature (°C), (G) temperature range (°C), (H) range of latitude (°), and (I) latitudinal midpoint (°) for both groups and for all other salmonid species known to occur globally. Subspecies of established and failed invaders are from Miller and Alcorn (1946). Bold subspecies are those that are not recognized by FishBase.

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Building on Beverton's legacy: life history variation and fisheries management

This is a diverse group of studies showing how natural selection can produce phenotypic and genetic shifts in fish life history traits, and how life history traits can in turn provide information about fish population dynamics. The articles highlight the potential for exploitation to cause rapid shifts in life history traits, which may be detrimental to future harvests or even to species survival. Leading researchers from both Europe and North America have contributed to this series, illuminating a series of topics that, in many cases, were first explored by Ray Beverton.

[Construire sur l'héritage de Beverton : variation du cycle biologique et gestion des pêches]

Cette série d'études variées illustre la façon dont la sélection naturelle peut causer des variations génétiques et phénotypiques dans les caractéristiques du cycle biologique des poissons et la façon dont ces caractéristiques peuvent, à leur tour, nous fournir des données sur la dynamique des populations de poissons. Les articles de cette série traitent des effets potentiels de l'exploitation pouvant mener à des variations rapides dans les caractéristiques du cycle biologique et entraîner des répercussions néfastes sur les récoltes futures ou même la survie des espèces. Des chercheurs émérites de l'Europe et de l'Amérique du Nord ont contribué à cette série faisant état de sujets qui, pour la plupart, ont été initialement explorés par Ray Beverton.

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Erin S. Dunlop, Brian J. Shuter, and Mark S. Ridgway	**844–853**	Isolating the influence of growth rate on maturation patterns in the smallmouth bass (*Micropterus dolomieu*)
John D. Reynolds, Thomas J. Webb, and Lorraine A. Hawkins	**854–862**	Life history and ecological correlates of extinction risk in European freshwater fishes
Leah R. Gerber, Selina S. Heppell, Ford Ballantyne, and Enric Sala	**863–871**	The role of dispersal and demography in determining the efficacy of marine reserves
PERSPECTIVE		PERSPECTIVE
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Building on Beverton's legacy: life history variation and fisheries management

[Construire sur l'héritage de Beverton : variation du cycle biologique et gestion des pêches]

	INTRODUCTION	INTRODUCTION
Brian J. Shuter and Peter. A. Abrams	725–729	Introducing the symposium "Building on Beverton's legacy: life history variation and fisheries management"
	PERSPECTIVE	PERSPECTIVE
David O. Conover, Stephen A. Arnott, Matthew R. Walsh, and Stephan B. Munch	730–737	Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*)
	ARTICLES	ARTICLES
B.J. Shuter, N.P. Lester, J. LaRose, C.F. Purchase, K. Vascotto, G. Morgan, N.C. Collins, and P.A. Abrams	738–746	Optimal life histories and food web position: linkages among somatic growth, reproductive investment, and mortality
Pierre Magnan, Raphaël Proulx, and Michel Plante	747–757	Integrating the effects of fish exploitation and interspecific competition into current life history theories: an example with lacustrine brook trout (*Salvelinus fontinalis*) populations
Peter A. Abrams and Hiroyuki Matsuda	758–766	The effect of adaptive change in the prey on the dynamics of an exploited predator population
Michael D. Rennie, Nicholas C. Collins, Brian J. Shuter, James W. Rajotte, and Patrice Couture	767–780	A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower
Donald L. DeAngelis, Joel C. Trexler, and William F. Loftus	781–790	Life history trade-offs and community dynamics of small fishes in a seasonally pulsed wetland
David N. Reznick and Cameron K. Ghalambor	791–801	Can commercial fishing cause evolution? Answers from guppies (*Poecilia reticulata*)
S.B. Munch, M.R. Walsh, and D.O. Conover	802–810	Harvest selection, genetic correlations, and evolutionary changes in recruitment: one less thing to worry about?
Esben Moland Olsen, George R. Lilly, Mikko Heino, M. Joanne Morgan, John Brattey, and Ulf Dieckmann	811–823	Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*)

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